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Production of perennial vegetation in an oasis-desert transition zone in NW China - allometric estimation, and assessment of flooding and use effects

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Abstract

River oases at the southern fringe of the Taklamakan desert in NW China are surrounded by belts of spontaneous vegetation that protect the oases from sand drift. As an important source of forage, fuel and construction wood, this foreland vegetation is also a component part of the agricultural system of the oases but has been, and still is, destroyed through overuse. Within a broader study that aimed to provide a basis for a sustainable management of this foreland vegetation, biomass and production were studied in four vegetation types dominated either by *Alhagi sparsifolia*, *Calligonum caput-medusae*, *Populus euphratica*, or *Tamarix ramosissima* that were thought to occur under different regimes of natural flooding in the foreland of Qira (Cele) oasis, Xinjiang, NW China. Shoot biomass components were closely correlated to basal area (*Calligonum*, *Populus*, *Tamarix*) or shrub volume and projection area (*Alhagi*), enabling non-destructive estimation of stand biomass from shoot diameters or shrub dimensions with sufficient precision using allometric regression equations. Relationships between shoot basal area and biomass of the woody species (*Calligonum*, *Populus and Tamarix*) agreed with predictions by a theoretical model of plant vascular systems, suggesting that they are determined by hydraulic and mechanical requirements for shoot architecture. Average aboveground biomass densities of typical stands in late summer were 2.97 Mg/ha in *Alhagi*, 3.6 Mg/ha in a row plantation and 10.9 Mg/ha in homogenous stands of *Calligonum*, 22–29 Mg/ha in 22 year-old *Populus* forests and 1.9–3.1 Mg/ha in *Tamarix*-dominated vegetation. Annual aboveground production including wood and assimilation organs ranged from 2.11 to 11.3 Mg/ha in plantations of *Calligonum*, 3.17 to 6.12 Mg/ha in *Populus*, and 1.55 to 1.74 Mg/ha (based on total ground area) or 3.10 to 7.15 Mg/ha (in homogenous stands) in *Tamarix*. Production of *Alhagi* is equal to peak biomass. A thinning treatment simulating use by the local population enhanced productivity of *Calligonum*, *Populus and Tamarix*. A complete harvest of *Alhagi* in late August decreased production in the following year. An artificial flood irrigation treatment did not sufficiently increase soil water content except in the uppermost layer and had no clear beneficial effect on growth of the four species and even a negative effect on *Alhagi*, which was due to increased competition from annual species. As biomass and production with or without artificial irrigation were much higher than values expected for rain-fed desert vegetation at a mean annual precipitation of 35 mm, it is concluded that the existence of all vegetation types studied is probably based on permanent access to groundwater and that natural floods or precipitation do not contribute to their

water supply. The effects of agricultural groundwater use in the oasis on groundwater in the foreland of the oasis need further study. Sustainable use of this productive vegetation is possible but requires proper management.

Introduction

River oases on the southern fringe of the Taklamakan desert in Xinjiang, NW China, the second largest desert in the world, are surrounded by a belt of indigenous vegetation that functions as a shelter against drifting sand. This function of the vegetation belt is indispensable for the oases, as NW winds prevail at the southern fringe of the Taklamakan (Xia et al. 1993) and constantly transport silt from the desert towards the oases. The foreland vegetation is also a component part of the oases' agricultural system because it is a major source of forage, fuel and construction wood and is grazed by sheep, goats and camels.

As precipitation is scarce, natural floods of the rivers are thought to be the main source of water for this vegetation. These floods occur in summer due to snowmelt in the Kunlun Mountains, where the rivers originate. Today, some of that water is stored in reservoirs up-stream, much of it is used immediately for irrigation of arable land, and the remainder, if any, is diverted into the foreland of the oasis. It is thought that flood irrigation water infiltrates into the soil, is stored there, and supports growth of the foreland vegetation for a prolonged time after flooding. This assumption seems reasonable, as silt is the predominant particle size fraction and the soil thus has excellent water storage capacity.

The protective foreland vegetation is threatened by increasing overuse due to rapid population growth, and by an increasing use of water for irrigation, as agriculture shifts to more water-demanding crops. Due to excessive harvest and grazing, large areas are completely free of vegetation, with wind erosion and generation of shifting dunes as a consequence. In order to preserve the foreland vegetation as a valuable resource and to maintain its sand-fixing function it has to be protected, but as use will continue, the demand of users has to be considered. A sustainable management of this vegetation requires information on how much material may be removed without destroying the vegetation. However, virtually nothing is known about (a) biomass stores and annual production of this vegetation, (b) the effect of use on production, (c) the effects of flooding, or drought stress due to the lack of flooding, on growth of the plants, (d) the amount of water that is used by the plants, and how long the water that infiltrates into the soil during a flood irrigation ensures an adequate water supply.

Within the framework of a broader study, this work therefore aimed to determine biomass density and annual production with and without experimental flood irrigation, and with and without simulated use by complete harvest or thinning. The study focused on dominant vegetation types formed by plant species that are either important for the protective function of the vegetation belt or for use by the population. These were the native perennials *Alhagi sparsifolia* Shap. (Fabaceae), *Populus euphratica* Oliv. (syn. *P.diversifolia* Schrenk; Salicaceae) and *Tamarix ramosissima* Ledeb. (Tamaricaceae), and *Calligonum caput-medusae* Schrenk, which is native to Xinjiang, but not to the southern fringe of the Taklamakan desert.

Stands of these species are thought to occur under different flooding regimes, suggesting differences in water demand: On average, the *Alhagi* and *Tamarix* sites have been reached by natural floods every 3 years; the *Calligonum* site and the *Populus* site every 2 years since 1983.

We hypothesized that flood irrigation would increase the amount of plant-available water stored in the soil, which would in turn decrease drought stress and enhance productivity for a prolonged period after the flood irrigation. We further hypothesized that removal of individual shoots or ramets of woody species would increase productivity of the remaining shoots, which would in turn partly compensate for the removal of biomass. On the other hand we expected that a complete harvest of *Alhagi* plants in summer would decrease production in the following year. It is customary to hack Alhagi shrubs approx. 1 dm below the surface. This technique removes not only the aboveground parts, but also many renewal buds, which are on the stems just beneath

or at the soil surface. We hypothesized that this would impair the following year's growth much more than just the harvest *per se*.

With respect to production measurements, we hypothesized that plant biomass could be determined non-destructively from stem diameter or shrub volume, based on allometric regression equations. Production could then be calculated from annually repeated non-destructive biomass determinations. With data sets obtained to derive allometric regression equations, we also tested predictions by a general and simple mathematical model that describes plant shoots as branching networks that are subject to hydrodynamic and mechanical requirements (West et al. 1999). This model predicts that radius at the shoot base scales with shoot mass according to

$$\text{radius} \propto \text{mass}^{8/3}$$

which is equivalent to

$$\text{mass} \propto \text{area}^{4/3}$$

with area = cross-sectional area of shoot.

Objectives were thus to (a) establish allometric relationships between easily measured variables and biomass, (b) non-destructively determine stand biomass, (c) determine seasonal course and annual total of production of individual shoots and of stands, (d) determine effects of flood irrigation on production, and (e) determine effects of use in the local manner on production.

Methods

Location and ecological setting

The study was carried out near Qira (Cele) oasis (population 130,000), at 37°01′ N, 80°48′ E and at an elevation of 1365 m a.s.l. Qira is located 90 km E of Hotan at the southern fringe of the Taklamakan desert in Xinjiang Uighur Autonomous Region, NW China. The Taklamakan desert (337,000 km^2) is in the Tarim basin, one of the largest internal drainage basins in the world, which is surrounded by the alpine mountain ranges of the Pamir to the west (8611 m a.s.l.), the Tian Shan to the north (7450 m) and the Kunlun to the south (7712 m). Tributaries and ephemeral rivers entering the desert from these glaciated mountain ranges allowed the establishment of river oases along the desert margins, which mark the course of the ancient silk road. These rivers carry little water in winter, but, fed by snow melt, can flood large areas in summer, resulting in extensive water erosion, and relocating huge amounts of sediments (up to 193 kg m^{-3}, Gentelle 1992). The larger rivers can leave large flood plains several km wide after a summer flood. The river system of the Taklamakan has been constantly changing in historical times, with diversions and shifting beds.

As NW winds prevail in the western Taklamakan and NE winds in the east, aeolic sediments constantly accumulate at the southern margin, forming layers 200–500 m thick (Zhou 1993; Li et al. 1997).

Qira oasis is situated in the desert margin near the transition to the glacial alluvial fans extending northward from the foothills of the Kunlun mountains (Hövermann 1988; Jäkel 1990), which are approx. 50 km to the south. It is on average 10 km in diameter and is surrounded by a 5–10-km wide belt of sparse, spontaneous vegetation dominated by woody species (referred to as the foreland) (Bruelheide et al. 2003; Qong et al. 2002) that forms a transition zone to the open silt desert.

The Qira river originates in the Kunlun mountains. Its flow rate, like that of all other rivers in the southern Taklamakan, is lowest between March and May (9% of annual total), and highest between June and August (77%) (Zhou 1993). In dry years the river water is directed completely through the oasis and used for field irrigation, with the remainder draining into the desert through the irrigation channels that lead open-ended into the foreland on the west, north and east sides of the oasis. In years with higher river flow rates, some of the water is diverted before entering the oasis and runs several km into the desert through a system of ancient and recent river beds.

Climate

The climate is extremely continental, with cold, dry winters and hot, dry summers. Mean annual temperature is 11.9 °C. The lowest air temperature recorded in the foreland vegetation of Qira in 2000 was −18.7 °C on January 18; the highest air

temperature was 40.6 °C on July 13. The annual potential evaporation is approx. 2600 mm and the annual sum of precipitation is 35.1 mm (Xia et al. 1993). The growing season of all species begins in mid April and ends in October. The last day of spring with frost was March 28 in 1999 and March 26 in 2000. The first frost in autumn was recorded on October 15 (−0.41 °C) in 1999 and on October 14 (−0.15 °C) in 2000. During May to September of 1999 and 2000, mean air temperatures were 24.0 and 23.8 °C, sums of shortwave radiation were 3097 and 3074 MJ m^{-2}, and mean vapor pressure deficits between 8 and 16 h solar time were 3.16 and 3.19 kPa, respectively.

Soil

Soils underneath the different vegetation types studied are very uniform. Silt is the predominant grain size fraction, with >87% in all 35 plots sampled around Qira oasis. No soil aggregates were found in any soil depth in the experimental plots. There is no differentiation into horizons within the soil profile, neither visually nor physically. Chemically, soils are also uniform among the study sites except a slightly higher Ca^{2+} content in the upper few cm in the *Alhagi* site, probably due to accumulation of *Alhagi* litter, which is rich in calcium, and a higher sodium content in the uppermost soil layer of the *Tamarix* plots that is probably caused by accumulation of shed *Tamarix* short shoots, which have a high Na^{+} content (unpublished data).

Virtually no fine roots were found in the *Alhagi* and *Calligonum* sites upon digging to 3.5 m depth and drilling to 8 and 4.5 m, respectively. Live fine roots were only found in the capillary fringe above the groundwater table in the *Tamarix* and *Populus* plots, where in mid-April groundwater was found at 5.7 and 3.6 m, respectively.

Soil water contents in different depths were measured regularly during the 2-year experimental

Table 1. Parameters of linear allometric regression equations that predict natural logarithms of dry weights of biomass components (and leaf area for *P. euphratica*) from natural log of shoot basal area or shrub volume (*A. sparsifolia*).

Predictor (units)	Range	Predicted variable	R^2	Offset	Slope	CF	*n*
A. sparsifolia							
Shrub *V* (cm^3)	0.01–1.90	Shrub DM (g)	0.96	−7.745	1.035	1.026	50
projection area (cm^2)	0.07–2.43	Shrub DM (g)	0.95	−7.407	1.403	1.062	50
C. caput-medusae							
basal $area_{0.1\ m}$ (mm^2)	5.2–1581	Shoot DM (g)	0.98	−1.405	1.306	1.038	56
		shoot DM, fixed slope	0.98	−1.535	4/3	1.038	56
		leaf DM (g)	0.95	−0.828	1.010	1.058	56
		total DM (g)	0.98	−0.550	1.208	1.034	56
P. euphratica							
basal $area_{1.3\ m}$ (cm^2)	7.2–127	Bole DM (g)	0.97	3.883	1.253	1.013	15
		Bole DM, fixed slope	0.97	3.595	4/3	1.034	15
		Branch DM (g)	0.90	3.762	1.080	1.045	15
		Leaf DM (g)	0.86	2.916	0.989	1.057	15
		Wood DM (g)	0.97	4.491	1.194	1.018	15
		Total DM (g)	0.96	4.663	1.173	1.020	15
		Leaf area (m^2)	0.86	−1.535	0.943	1.052	15
		Bole *V* (dm^3)	0.98	−2.502	1.360	1.016	15
		Bole *V*, fixed slope	0.98	−2.407	4/3	1.014	15
		Bole *V*, $d > 0.07$ m (dm^3)	0.89	−4.153	1.662	1.062	15
T. ramosissima							
Basal $area_{0.1\ m}$ (mm^2)	12.8–511	Shoot DM (g)	0.98	−1.647	1.330	1.018	50
		Shoot DM, fixed slope	0.98	−1.662	4/3	1.018	50
		Leaf DM (g)	0.92	−1.053	1.015	1.045	50
		Total DM (g)	0.98	−0.823	1.232	1.019	50

Shrub volume of *Alhagi* was calculated as a sphere, shrub projection area as a circle. CF = factor correcting for bias in regression of log transformed data; *V* = volume, *d* = diameter, DM = dry matter, shoot = aboveground woody plant parts, leaf = assimilation organs.

Table 2. Biomass density of *Alhagi sparsifolia* subplots at the peak of biomass development in summer 1999 and 2000.

Irrigation	Use	Biomass 1999, Mg/ha	Biomass 2000, Mg/ha	Between years ($p < 0.0085$)
D	N	2.10 ± 0.22 b	1.70 ± 0.23 a	0.0513 n.s.
	R	3.85 ± 0.33 a	1.54 ± 0.09 a	< 0.0001*
	U	2.97 ± 0.34 ab	1.53 ± 0.15 a	0.0006*
F	N	1.40 ± 0.34 B	0.42 ± 0.12 B	0.0384 n.s.
	R	2.20 ± 0.23 BA	0.96 ± 0.19 BA	< 0.0001*
	U	3.23 ± 0.30 A	1.51 ± 0.17 A	< 0.0001*

Means ± 1 SE (n = 8–10 sample squares). For each year separately, small letters indicate differences between uselevels in D subplots and capital letters between use levels in F subplots. Asterisks in the last column indicate significant differences of subplot biomass between years (paired t-tests with Bonferroni correction).

phase and were reported, together with a detailed description of the project, in Thomas et al. (2000a).

Vegetation

Native *Alhagi sparsifolia* Shap. (camelthorn, *Fabaceae*) is a spiny, perennial herb with few leaves, about 1 m tall; it is probably synonymous to *A. maurorum* Medik., *A. pseudalhagi* (M. Bieb.) Desv. (*A. camelorum*), and *A. kirghisorum* Schrenk. Near the oasis, this species spontaneously forms pure, dense stands with on average one shrub per square meter. The total area surveyed was approx. 4000 m^2. No regeneration of *Alhagi* was observed during three years. No fine roots were found upon digging to 3.5 m and drilling to 8 m. In addition to *Alhagi*, few individuals of *Launaea divaricata* (Desf.) Andreanszky [syn. *Scorzonera divaricata* (Turcz.)] (Asteraceae), *Phragmites australis* (Cav.) Steudel (Poaceae) and *Karelinia caspica* (Pall.) Less. (Asteraceae) occur in the site. There are reasons to believe that the *Alhagi* areas were fields that were abandoned several decades ago. Their relief is unusually level with only occasional small dunes and they are adjacent to present farmland. Especially in the spring, when plant tissue including spines is still soft, these stands are intensely grazed. Additionally, these stands were probably harvested more or less annually. Harvest is prohibited by law within 3 km of the oasis, but according to our observation this law is frequently violated. This can also be inferred from the observation that only few dead shrubs were found in part of that area, while in the fenced plots we found that dead shrubs (all aboveground parts regularly die in winter), remain for at least 2 years.

Calligonum caput-medusae Schrenk (*Polygonaceae*) is a 2–3 m tall leafless shrub with young shoots serving as assimilation organs. It is native to Xinjiang, but not to the southern fringe of the Taklamakan. Stands planted as shelter vegetation are nonetheless grazed and cut as fuel. Experimental plots of *Calligonum* were established in pure stands planted in 1985. Stands on two adjacent dunes that were not irrigated were homogenous, but the plot to be irrigated had a row structure with on average six meters of open space between rows. There was little horizontal vegetative spread between these rows, even though the stand was planted more than 15 years ago and the largest shoots were larger than 7 cm in diameter. In the stands on dunes, continued burial by sand probably caused the change from the original rows to homogenous structure as *Calligonum* grew with the rising surface, without horizontal spread by runners or tillers from rootstocks being necessary. No fine roots were found upon digging down to 3.5 m and drilling to 4.5 m in any stand. The plots did not differ from each other in terms of soil texture, nutrients and water (Foetzki 2003).

The native tree *Populus euphratica* Oliv. (syn. *diversifolia* Schrenk, *Salicaceae*) has narrow, willow-like as well as broad, poplar-like leaves. The stands investigated are remnants of forests that formerly covered a much larger area but are gone today due to logging, according to oral information (Zhang Henian, personal communication) and to published evaluations of aerial photographs and field observations (Bruelheide et al. 2003) including frequent sightings of tree stumps as well as partly buried layers of leaves in the foreland several km away from the oasis. Experimental plots were established in dense stands of 22-year-old, 4–6 m high trees (Tables 3 and 4). Trees frequently grew in

Table 3. Initial biomass density in subplots of *Calligonum*, *Populus* and *Tamarix*, before treatments were applied.

Irrigation	Use	Wood, Mg/ha	Assimilation organs, Mg/ha	Production, Mg/ha	%
Calligonum					
D	N	8.82 ± 3.40	2.91 ± 0.85	11.25 ± 2.38	96.9
	U	7.79 ± 2.26	2.65 ± 0.74	4.43 ± 1.19	42.7
F	N	2.70 ± 0.80	0.89 ± 0.22	2.09 ± 0.50	59.2
	U	3.00 ± 1.70	0.98 ± 0.50	2.15 ± 0.97	54.8
Populus					
D	N	21.5 ± 0.89	2.20 ± 0.07	3.14 ± 0.11	13.2
	U	19.3 ± 0.82	1.90 ± 0.07	3.00 ± 0.11	14.1
F	N	30.4 ± 1.63	2.78 ± 0.13	6.11 ± 0.33	18.4
	U	21.9 ± 1.35	2.06 ± 0.11	4.34 ± 0.21	18.1
Tamarix					
D	N	1.72 ± 0.85	0.91 ± 0.45	1.34 ±0.70	51.1
	U	2.40 ± 0.94	1.21 ± 0.42	1.76 ±0.66	49.2
F	N	0.27 ± 0.19	0.12 ± 0.09	0.19 ±0.31	47.4
	U	2.18 ± 1.01	1.14 ± 0.52	3.30 ±1.57	99.1

Production is shown for the growing season 1999, the year the flood irrigation was applied, but before use treatments were applied. Production as percentage of initial biomass facilitates comparisons of treatments despite different initial biomass densities.

Table 4. Structure of *Populus euphratica* stands before treatments were applied.

Irrigation	Use	Stand density, trees/ha	LAI, m^2/m^2	Basal area, m^2/ha	Bole volume, m^3/ha
D	N	3425	2.2 ± 0.07	11.7 ± 0.4	36.1 ± 1.72
	U	2517	1.9 ± 0.06	10.2 ± 0.36	33.4 ± 1.60
F	N	2769	2.7 ± 0.12	14.9 ± 0.68	55.8 ± 3.38
	U	2313	2.0 ± 0.10	11.0 ± 0.57	39.4 ± 2.76

Means ± 1 SE of 111–151 trees. LAI = leaf area index.

clusters of two to five, but stems in a cluster did not obviously originate from a common stump. All trees (but one) within an area of 4 ha belong to one genet (Bruelheide et al. 2003). In the plot that was later irrigated, stand density was lower than in the non-irrigated plot (Table 3).

Native *Tamarix ramosissima* Ldb. (saltcedar, *Tamaricaceae*) is a 2-m tall shrub in the area, in other areas also a tree. The experimental plots (total area 5000 m^2) were in spontaneous *Tamarix* shrub land typical for the area within a few km from the oasis. It includes areas covered by dense, homogenous bushes of *Tamarix* as well as areas with mostly bare soil and few *Karelinia caspica*, *Phragmites australis* and *Alhagi* plants. Approximately 20–50% of the ground area was covered with *Tamarix* stands.

Irrigation treatment

Of the total annual amount of river water, 77% reaches the oasis between June and August; this is not only the time when natural flooding occurs, but has also traditionally been the time when excess water was diverted to the foreland. Irrigations were thus scheduled during this time to simulate and to study the effects of natural floodings and traditional management. Within each of the four vegetation types, two (*Populus* and *Tamarix*) or three (*Alhagi* and *Calligonum*) plots ranging in size from 850 to 2500 m^2 were established and fenced. One was irrigated by artificial flooding in summer 1999 and the other plot(s) received no irrigation during the investigation period. For the flooding, water from the regular irrigation channel system of the oasis was led to the sites in simple, improvised ditches that were dug into the soil or by canals formed by dams made of soil. The *Alhagi* plot was flooded with approx. 0.4 m^3/m^2 on June 21, 1999. For the other plots, the quantity of irrigation water could not be determined. In each case, water covered the entire plot for at least 8 h. The *Calligonum* plot was flooded on July 22, the *Tamarix* and *Populus* plots on August 5 and 6, 1999. Biomass and production were determined in the

year the irrigation was applied, and in the following year.

Use treatment

Subplots of both irrigated and non-irrigated plots were subjected to an experimental treatment simulating use in the local manner at the end of the first growing season. The irrigated and non-irrigated plots each were divided into two (*Calligonum*, *Populus*, *Tamarix*) or three (*Alhagi*) subplots ranging in size from 450 to 850 m^2. In one subplot, plants were allowed to grow without harvest. In the other, a use treatment was applied August 24–29, 1999 (*Alhagi*), September 7/8, 1999 (*Calligonum*), October 25, 1999 (*Populus*) or September 3/4, 1999 (*Tamarix*). This treatment was designed to best simulate the local way of use of each species as much as possible. In *Alhagi*, all plants were removed by hacking with a local type of hoe designed and used for this and other specific purposes by the Uighur farmers into the soil underneath each shrub, thereby cutting the stem approx. 1 dm below the soil surface. An additional, more careful way of use ('reduced use') was applied in a third subplot in which plants were cut just above the soil surface with gardener's scissors.

In *Calligonum*, we first determined current biomass density in 2 m × 2 m sample plots that had been established for determination of biomass (see below) in April 1999 and then cut individual shoots in the sample plots, beginning with the largest diameters, until half the biomass was removed from each sample plot. The shrubs neighboring the sample plots within 2 m on each side were treated in the same way.

In *Populus*, the target was to decrease stem density to half its original value and at the same time to make stem distribution more uniform. First, stem density in the 'use' subplot was determined. Then, the subplot was divided into 5 m × 5 m squares. In each square, a number of stems were cut in order to establish the target density. If the original density of a subplot was already lower than the target density, then this was compensated by allowing a higher density in the adjoining squares. Stems frequently grew in clusters of 2–5. If there was a choice, it was preferred to cut some stems out of those clusters (without removing a complete cluster) instead of cutting solitary trees. On the non-irrigated plot, 66 out of 151 trees were cut. On the irrigated plot, 54 out of 111 trees were cut.

In *Tamarix*, the number of shoots was considered too high to do any of the above and stands were more evenly structured, so all shoots were cut in strips of 1 m across the subplot, leaving strips of 1 m in between.

Allometric regression equations

Alhagi

Usually, plant biomass is estimated most precisely from basal area; however basal area is difficult to measure in *Alhagi*, because shrubs are very spiny and already branch below the soil surface, so that shoots are not easily accessible for measurements. Therefore, we tried to establish a regression equation with which biomass can be estimated from shrub crown volume (Nikolaev and Baimyradov 1987; Uso et al. 1997). 50 shrubs were selected to cover the range of shrub sizes occurring in the plots. For estimating shrub volume, the longest horizontal extent of the shrub, the longest extent perpendicular to that, and the height of the highest twig was measured. Shrub basal area at the soil surface was also determined by measuring basal diameters of all shoots of each shrub. Shrubs were weighed fresh and dry mass was calculated from the water content of oven-dried subsamples.

Calligonum and Tamarix

Fifty-six shoots of *Calligonum* and 50 shoots of *Tamarix* were selected to cover the range of shoot diameters occurring in the plots. For each shoot, basal areas 0.1 m above the soil surface were determined by measuring two diameters perpendicular to each other. Assimilation organs (new, green shoots in *Calligonum*, green short shoots in *Tamarix*) and woody parts of each shoot were immediately stored in separate plastic bags and were weighed fresh within 4 h. All dry masses were determined from fresh masses and water contents of oven-dried subsamples that were taken at the time of fresh-mass determination.

Populus

Fifteen trees covering the range of diameters occurring in the stands were harvested. The trees were divided into 2-m segments. Trunk diameter

was measured at the soil surface, at 0.1 and 1.3 m, and at each segment. Total trunk length (main axis >0.1 m circumference) and length of the trunk segment larger than 0.07 m diameter ('coarse wood') was measured. Trunks were weighed immediately. Pieces of 0.1 m length were cut off at the base and at the top of the trunk and were stored in plastic bags. All leaves of each segment were collected immediately and were stored in plastic bags. All branches from each segment were cut off and weighed separately. Trunk dry mass was determined from trunk fresh mass and water content of the pieces that were cut from the top and base. Wood density and bark fraction was also determined from these pieces. Total trunk volume was calculated as the sum of the volumes of all segments >0.1 m circumference. Branch and leaf dry masses of each two-meter segment were calculated from fresh masses and water contents of oven-dried subsamples. Specific leaf area of leaf subsamples from each segment was determined by measuring leaf area with a flatbed scanner using Delta-T image analysis software, and subsequent drying. All oven drying was made in a forced-drought oven at 60 °C for at least 2 days, or until mass was constant in the case of woody samples.

Factors that were varied in optimizing allometric regression equations were: mathematical model (linear, power, or polynomial), data transformation (no transformation or transformation to natural logarithm), independent variable (basal area at 0.1 m, basal area directly above ground surface, or combination of basal area and height). For *Alhagi*, several ways of calculating shrub volume or shrub projection area as independent variable were compared (two-dimensional: circle, ellipse and rectangle; three-dimensional: sphere, sphere cap, cube, etc.).

Without data transformation, most data sets did not meet all requirements for regression analysis, therefore all data were transformed to their natural logarithm and linear equations were fitted using least-squares procedures. Factors (CF) correcting for the bias introduced by logarithmic transformation were calculated according to Sprugel (1983):

$$\mathrm{CF} = \exp\,(\mathrm{SEE}^2/2)$$

with SEE = standard error of estimate. Regressions were tested for significance by ANOVA, equation parameters by *t*-tests. Regression was assumed if p was <0.05. Normal distribution of data was checked using the Kolmogorov–Smirnov test. Normal distribution was assumed if p for H1 was >0.05. Homogeneity of variances was tested using the Levene Median test ($p > 0.05$). To test for autocorrelation of residuals, the Durbin–Watson coefficient was calculated. Equations with a coefficient between 1.5 and 2.5 were accepted. All R^2-values shown were routinely adjusted for the degrees of freedom of the sums of squares associated with R^2. This adjustment is necessary if equations with different numbers of parameters are compared, as in the case described below. R^2-values are slightly higher without this adjustment. All statistical tests of regressions described above were made using SigmaPlot 2000 software (SPSS Science, Chicago, USA).

In order to test whether the exponent of 4/3 in the relationship between shoot mass and basal area that was derived from predictions by a theoretical model fits the present data, slope and offset of the equations for shoot masses of *Calligonum*, *Populus* and *Tamarix* were either allowed to vary freely, or the slope was fixed to 4/3 (the value predicted by the theoretical model) and only the offset was allowed to vary. Differences between free parameter estimates and fixed slope and corresponding offsets were tested for statistical significance with *t*-tests (Lozan 1992).

Determination of aboveground biomass density and production

For the woody species (*Calligonum*, *Populus*, *Tamarix*), which all have deciduous assimilation organs, production is defined as the sum of wood increment during one growing season and total leaf mass in that growing season. Production of flowers and fruits is not considered in this calculation but may play a significant role for *Calligonum*, which produces many large seeds.

In *Alhagi*, ten sample plots (4 m × 4 m) were spaced evenly in each of the irrigation/use subplots except in the irrigated, not used subplot, in which only eight sample plots were established. In the 'no use' subplots, biomass was determined non-destructively in both years. For this purpose, aboveground length, width and height of each *Alhagi* shrub was measured and biomass was calculated from these dimensions with the

appropriate regression equation. In the 'use' and 'reduced use' subplots, all shrubs in the sample plots were harvested at the same time the use treatment was applied in summer 1999 and their dry mass was determined based on their fresh mass and the water content of subsamples that were dried at 60 °C for several days. In summer 2000, biomass was determined non-destructively in the same manner as in the 'no use' subplots. Treatment biomass and production was calculated as sample plot means. Peak biomass density is equal to production, because all aboveground parts die each winter.

In *Calligonum*, biomass determination was based on 2 m × 2 m sample plots in the non-irrigated subplots (five in the 'no use' and six in the 'use' subplot) that were spaced evenly on the plots in order to statistically represent the total subplot area. In the irrigated 'no use' and 'use' subplots, which together covered an area of 50 m × 50 m, 25 sample plots of 10 m length and 2 m width were established in five rows spaced evenly over both subplots and laid out perpendicular to the shrub rows in order to account for the systematic, non-random row structure of the stand. There were 15 sample plots in the 'no use' and 10 in the 'use' subplot. These 25 sample plots covered 20% of the total area of the irrigated subplots.

Diameters of all shoots in all sample plots were measured with caliper rules once in April 1999 and initial biomass was calculated from basal area with allometric regression equations. Additionally, 5–15 shoots (depending on the number of shoots in the sample plot) were selected in each sample plot to represent the diameter distribution of the respective sample plot and were marked. Further biomass and production estimates were based on diameter increase of these shoots. Their total number included into calculations were 37 (no irrigation, no use), 47 (no irrigation, use), 90 (irrigation, no use), and 58 (irrigation, use). In April 2000 and 2001, diameters of these marked shoots were measured again and the shoots were distributed into seven or eight equally sized classes according to their basal area, and for each class and each year, a mean relative basal area increase (i.e., basal area increase in relation to initial basal area) was calculated. Basal area increment of all shoots in the sample plots was then calculated based on their initial basal area and the relative basal area increase of the appropriate class of marked shoots. New biomass of sample plots was calculated from new basal areas of all shoots and allometric regression equations. Annual production was calculated as annual wood increment plus total mass of assimilation organs in the respective growing season. Treatment production was calculated as mean sample plot production.

Populus

In April 1999, all trees in all plots were marked and their circumference at 1.3 m height was measured with a tape measure. Measurements were repeated in April 2000 and 2001. Biomass fractions were calculated from basal areas using allometric regression equations. Production was calculated as annual wood increment plus total leaf mass.

Tamarix

Sample plots of 1- m^2 size were spaced evenly on the plots; there were 20 on the irrigated plot, and 16 on the non-irrigated plot. In late April 1999, dead shoots were removed and diameters of all shoots in all sample plots were measured with caliper rules, new shoots separately. Sample plot biomass was calculated from shoot diameters and allometric equations. In April 2000 all diameters were measured again, live and dead shoots separately, and dead shoots were removed. This procedure was repeated in April 2001. All biomass densities were calculated from these sample plots. Production in the growing season 1999 was calculated as wood increment between April 1999 and 2000 plus total mass of assimilation organs (short shoots) in 1999. To better monitor the effects of thinning in September 1999 on growth during summer 2000, in all sample plots a number of shoots were selected in April 2000 to represent the range of shoot diameters occurring in the sample plots. These shoots were marked and their diameters were measured. That measurement was repeated in April 2001.

Seasonal course of growth

The seasonal course of average shrub biomass of *Alhagi* was determined from five sequential harvests of twelve randomly selected shrubs per harvest.*Calligonum*: the seasonal course of diameter increase of six shoots was measured with permanently installed fine scale increment tapes that

allow measurements of diameter increment at a resolution of 0.08 mm. *Populus*: the seasonal course of wood production was estimated from the seasonal pattern of stem diameter increase that was measured with fine scale increment tapes that allow measurements of diameter increment at a resolution of 0.08 mm.

Statistical analysis of treatment effects

Samples were tested for normal distribution by calculating the Shapiro–Wilk *W*-statistic ($p > 0.1$) (SAS proc univariate, The SAS Institute, Cary, NC, USA). If normal distribution was confirmed, data were analyzed by ANOVA and Scheffe's test (both SAS proc glm); If not, the Kruskal–Wallis *H*-statistic was calculated and if significant, Wilcoxon rank sum tests were performed on samples (both SAS proc npar1way). Pairwise *t*-tests with Bonferroni correction were used for between-year comparisons.

Factors: (1) flood irrigation, (2) use. Levels of flood irrigation and abbreviations: not flooded = D ('dry'), flooded = F. Levels of use: no use = N, reduced use = R (*Alhagi* only), normal use = U.

Variables tested: (above ground) biomass of *Alhagi* (Table 2), radial increment of *Populus* stems (Table 5), relative biomass increment of *Calligonum* shoots (Table 6), absolute and relative basal area increment and biomass increment of *Tamarix* shoots (Table 7).

Results

Allometric regression equations

The equations presented in Table 1 are those that yield the best quality of fit in each case. All equations shown are statistically significant ($p < 0.001$) and meet requirements for regression analysis with respect to normal distribution, homogeneity of variances, and autocorrelation of residuals. Shrub volume of Alhagi was closest correlated to biomass when calculated as a sphere, with mean of shrub length, width and height as diameter. Of the two-dimensional predictors for *Alhagi* biomass, projection area calculated as a circle with mean of shrub length and width as diameter gave the best quality of fit. Basal area at 0.1 m height was a better predictor than basal area at ground level for the woody species. Also, as in many other studies, inclusion of height as an independent variable did not improve regressions for the woody species. For shoot (trunk) mass of the woody species *Calligonum*, *Tamarix* and

Table 5. Radial growth of *Populus euphratica* in the experimental plots in 1999 and 2000.

Year	Irrigation	Use	Radial increment, mm	Irrigation			Use		
				No use	Use	Pooled	No irrigation	Irrigated	Pooled
1999	D	N	0.56 ± 0.04	A			a		
		(U)	0.79 ± 0.06		A		b		
		N + (U)	0.65 ± 0.03			A			
	F	N	1.66 ± 0.08	B				a	
		(U)	1.65 ± 0.15	B				a	
		N + (U)	1.66 ± 0.07			B			
	D + F	N	1.11 ± 0.06						a
		(U)	1.22 ± 0.11						a
2000	D	N	0.81 ± 0.04	A			a		
		U	1.10 ± 0.09		A		b		
		N + U	0.92 ± 0.04			A			
	F (1999)	N	0.95 ± 0.07	A				a	
		U	1.51 ± 0.10		B			b	
		N + U	1.11 ± 0.06			B			
	D + F	N	0.88 ± 0.06						a
		U	1.31 ± 0.09						b

Means ± 1 SE of 59 to 222 trees. Different letters indicate significant differences (ANOVA and Scheffe's test, $p < 0.05$). Flood irrigation was applied in August 1999. (U) = plots to be thinned, before thinning, U = the same plots after thinning in autumn 1999.

Table 6. Growth of individual shoots of *Calligonum caput-medusae* before (1999) and after (2000) a thinning treatment simulating use in the local manner.

Irrigation	Use	Biomass increment 1999		Biomass increment 2000		*p*
		g/shoot	% of initial	g/shoot	% of initial	
D	N	135 ± 39.5 a	85 ± 12 a	51.6 ± 13.5 a	28 ± 5 a	< 0.0001
	U	29.4 ± 8.77 b	30 ± 8 b	42.0 ± 9.70 a	41 ± 9 a	0.4103
F	N	80.1 ± 19.0 ab	54 ± 7 ab	79.8 ± 27.6 a	20 ± 4 a	< 0.0001
	U	70.7 ± 20.4 ab	58 ± 11 ab	83.7 ± 22.4 a	92 ± 49 a	0.5519

Means ± 1 SE, n = 44–101 shoots. F = flood irrigation in July 1999. U = thinning in autumn 1999. Values marked with the same letter do not differ significantly between treatments. p = error level for comparison of relative increment between years.

Table 7. Effect of thinning on growth of individual shoots of *Tamarix ramosissima* during the growing season 2000.

Irrigation	Use	Basal area increment		Dry mass increment
		mm^2	% of initial value	% of initial value
D	N	6.8 ± 1.6 a	24 ± 10 a	30 ± 13 a
	U	19.7 ± 4.2 b	58 ± 13 b	73 ± 17 b
F (1999)	N	12.5 ± 2.2 a	27 ± 5 a	34 ± 6 a
	U	16.6 ± 2.6 a	65 ± 11 b	80 ± 13 b
D + F pooled	N	9.2 ± 1.4 a	25 ± 6 a	32 ± 8 a
	U	18.2 ± 2.5 b	61 ± 8 b	77 ± 11 b

Means ± 1 SE, n = 18–25 shoots. U = thinning performed in September 1999. Within each irrigation level (D,F), values marked with the same letter do not differ significantly between use levels N and U.

Populus, free estimates of slopes were not significantly different from slopes forced to the value of 4/3 that was predicted theoretically, and neither were the corresponding offsets. Also, the quality of fit of the equations with slope fixed to 4/3 is the same as that of the equations with freely estimated parameters (Table 1). Thus, these data are in agreement with predictions made by the theoretical model of plant vascular systems.

Biomass density

Alhagi

Aboveground biomass density was 2.1–3.9 Mg/ha with some variation between subplots (Table 2). The total area surveyed was approx. 4000 m^2. *Calligonum*: Initial biomass density in the homogenous stands on dunes was quite uniform between the two adjacent dunes that were not irrigated but was much lower in the row-structured plot that was later irrigated (Table 3). *Populus*: In the plot that was later irrigated, leaf area index (LAI), basal area, bole volume (Table 4) and biomass before the experiment were higher than in the non-irrigated plot (Table 3). *Tamarix*: Biomass densities of the subplots were quite variable if expressed per unit ground area (Table 3), due to the inhomogeneous distribution of *Tamarix* bushes. However, within the *Tamarix* bushes, total biomass densities were quite uniform (720 ± 188 and 621 ± 88 g/m^2 in the non-irrigated and irrigated plots, respectively). Assimilation organs accounted for approx. 34% of the total biomass.

Production

Averaged over all treatments, production was quite uniform among the C_3 species, but production of *Calligonum*, the only C_4 species, was somewhat higher than that of the other species (Table 3). Also in this species, production varied to a large extent between the non-irrigated subplots, despite their similar stand densities (Table 3) and similar locations on adjoining dunes: Production of *Calligonum* in the 'use' subplot was only 39% of that in the 'no use' subplot. The only obvious difference between the subplots is that the less productive one is on a 5 m higher dune.

Average production for these stands in 1999 was 7.5 Mg/ha (wood and assimilation organs), and wood mass increment was 3.7 Mg/ha, or 45% of initial wood mass.

Bole volume increment of *Populus* corresponding to production values for non-used subplots in Table 3 was 1.65–6.53 m^3/ha in 1999, and 2.67–4.02 m^3/ha in 2000 for non-irrigated and irrigated stands, respectively. Growth of the 'no use'/'no irrigation' stand was very low in 1999, but radial increment increased by 45% in 2000 (Table 5). Observations on felled trees showed that tree ring width varied up to threefold in consecutive years in both stands, indicating large year-to-year variations of productivity.

Production of *Tamarix* in 1999 comprised 0.36 Mg/ha wood and 1.19 Mg/ha assimilation organs (short shoots) in the non-irrigated subplots. On a relative basis, average production of the non-irrigated subplots was 50% of the initial biomass and was thus in the range of that of *Calligonum* (Table 3). The area on which these numbers are based includes homogenous *Tamarix* stands as well as non-vegetated, bare soil; production in homogenous, non-irrigated *Tamarix* stands was 3.1 ± 0.47 Mg/ha in 1999, comprising 0.71 ± 0.19 Mg/ha wood and 2.39 ± 0.28 Mg/ha assimilation organs.

Production estimates for the growing season 2000 based on subplot inventories indicated negative production in some cases and were not reliable because we found proof for harvest of shoots by farmers or goatherds in sample plots, despite the fact that the plots were fenced. No harvest in experimental plots was observed in 1999. An example may show the effect of this kind of disturbance on experimental results: one shoot of 18 mm diameter made up 31% of the biomass (825 g/m^2) in one of the sample plots. That shoot was cut between April 2000 and 2001, and a negative production estimate ensued, despite a 40% biomass increase of the remaining shoots. However, production during summer 2000 can be estimated reliably from the growth of shoots that were marked and measured in April 2000. On average, dry matter increase of marked shoots in the non-irrigated, not used subplot during 2000 was 9.3 g per shoot, or 30% of their initial biomass in April 2000, and was thus considerably higher than the 17% that were measured on that subplot in 1999 (data for total biomass increment not shown). However, these numbers are based on different methods, and production during summer 2000 reduces to only 18% if it is taken into account that shoots of different diameters had different growth rates, and that the diameter distribution of those 25 marked shoots differed from that of the entirety of the shoots in the sample plots. The production estimate of 18% for 2000 was calculated by distributing marked shoots into five equally sized basal area classes and applying average growth rates of the respective basal area class to all individual shoots that were present in the sample plots in April 2000.

Seasonal course of growth

Alhagi

In both years, the first sprouts were seen in mid-April. Shrub biomass increased rapidly, and values among the June, August and September harvests in 1999 were not significantly different, indicating that maximal shrub mass was reached already in June and remained constant until September (Figure 1). In 2000, shrub mass appears to have increased more slowly; however, as in 1999 the June to September data are not significantly different.

Calligonum

In 1999, radial growth of *Calligonum* shoots measured at 0.1 m shoot height progressed at an almost constant rate from May through August and ceased in early September (Figure 2); however, July to October values were not significantly different. The pattern in 2000 was similar except

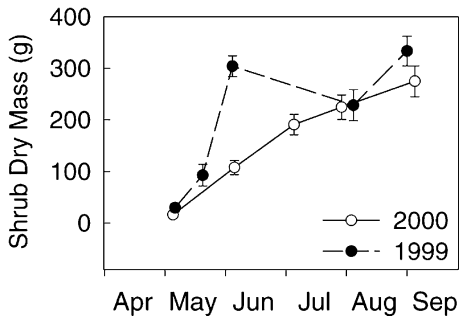

Figure 1. Average shrub dry mass of *Alhagi sparsifolia* during the growing seasons 1999 and 2000 determined by sequential harvests of twelve shoots per harvest.

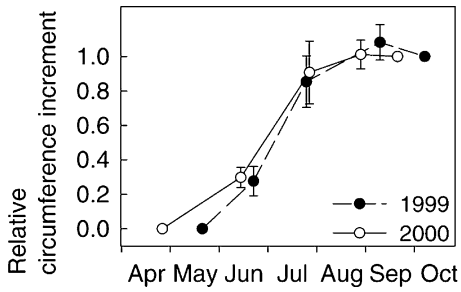

Figure 2. Seasonal course of circumference growth in *Calligonum caput-medusae* measured with fine-scale increment tapes. Means and standard errors of normalized diameters of six shoots. Standard errors of normalized diameters indicate differences in seasonal growth patterns between individual shoots.

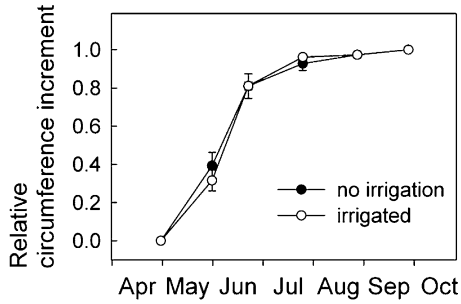

Figure 3. Populus euphratica: seasonal course of circumference increment measured with permanently installed fine-scale increment tapes. Means and standard errors of increment of 9–21 trees, normalized to the total annual increment for each tree. Standard errors indicate differences in seasonal growth patterns between individual trees.

that there was a slight trend for earlier cessation of growth. Mean final increment of stem radii in 'no use' stands varied between 1.5 ± 0.2 mm (irrigated plot) and 2.40 ± 0.4 mm (non-irrigated plot) in 1999 and between 0.87 ± 0.2 mm (irrigated plot) and 0.92 ± 0.2 mm (non-irrigated plot) in 2000, indicating that overall growth in 2000 was lower than in 1999 (means and standard errors of 35 to 101 shoots).

Populus

The rate of stem wood growth measured at 1.3 m height was highest in June, slowed down in July and had completely ceased at the time of the flood irrigation treatment in early August (Figure 3). Mean final increment of stem radius varied between 0.65 ± 0.03 mm (non-irrigated plot) and 1.66 ± 0.07 mm (irrigated plot).

Effects of flood irrigation

Alhagi

The flood-irrigation treatment was carried out on June 21 and was thus 1 month earlier than in the other species. In contrast to expectations, production of *Alhagi* was significantly lower in the flood-irrigated plot than in the non-irrigated plot in 1999 (Table 2). Dry mass averaged over the three 'use' subplots (the 'use' treatment was applied at the final harvest in 1999 and had thus no effect on these results) was 2.97 ± 0.21 Mg/ha in the non-irrigated and 2.34 ± 0.21 Mg/ha in the irrigated plot. At the same time several annual plant species (mostly Chenopodiaceae, mainly *Halogeton arachnoideum* and some *Salsola* spp) germinated and developed a dry mass of 1.94 ± 0.28 Mg/ha in the irrigated plot. Consequently, the total dry mass density in the irrigated plot (including *Alhagi* and the other species) was 4.65 ± 0.22 and was significantly higher than in the non-irrigated plot, where only *Alhagi* grew. While dry mass of these annual species was similar to that of *Alhagi*, they almost doubled *Alhagi* in fresh mass, indicating how strong their competition was: fresh mass of *Alhagi* was between 5.9 and 7.7 Mg/ha, and fresh mass of the Chenopodiaceae species alone was 9.7 to 13.2 Mg/ha!

In the following year, no more annuals grew in the irrigated plots, yet production was again significantly lower in the previously irrigated than in the non-irrigated plots. This was due to lower average shrub density and lower per-shrub mass in the previously irrigated plot: the number of shrubs had decreased from 0.78 shots/m^2 in 1999 to 0.42 shots/m^2 in 2000 and average shrub mass had decreased from 179 to 100 g. (Data on individual shrub mass and number of shrubs in 1999 are only available for the 'no use' subplot, in which biomass was determined non-destructively in both years.)

Calligonum caput-medusae

the stand was irrigated on July 22, 1999. Flood irrigation did not enhance growth in 1999 or in 2000: production in absolute terms, as well as in relation to initial biomass, was much higher in the non-irrigated than in the irrigated plot in 1999 (Table 3) and in 2000 (8.55 ± 1.97 Mg/ha in the non-irrigated plot and 2.29 ± 0.59 Mg/ha in the previously irrigated plot).

Populus

The flood irrigation treatment was applied on August 5, 1999. At that time, bole diameter growth had already ceased (Figure 3), but it was expected that flooding would enhance growth in the following year. Yet already in 1999 production of wood and leaves in the flood-irrigated plot was significantly higher than in the non-irrigated control, both in absolute and relative terms (Tables 3 and 5). This suggests a general difference in growth potential between the two plots. Production of wood and leaves in 2000, when treatment effects were actually expected, was again higher in the previously irrigated subplot than in the non-irrigated subplot (5.05 and 3.79 Mg/ha, respectively), however, on a relative basis, there was no difference between the plots (13.9% irrigated, 15.3% non-irrigated), suggesting that flood irrigation did not affect productivity. Radial growth of trees was significantly higher in the irrigated than in the non-irrigated plot in both years (Table 5), emphasizing the general difference in structure between the tree stands in the two plots.

There was a mixed response to flooding of the two irrigated subplots in *Tamarix*. Production in relation to initial biomass of the irrigated 'no use' subplot was similar to the non-irrigated subplots, but in the irrigated 'use' subplot, relative production was almost twice as high (Table 3). Biomass density of that subplot was much higher than that of the irrigated 'no use' subplot (Table 3), so that its high production still dominates the result when the two subplots are pooled (94 and 50% for irrigated and non-irrigated plots, respectively). Similar to these results, which are based on total ground area, production within homogenous stands (use subplots pooled) was also higher in irrigated than in non-irrigated plots (irrigated: 7.15 ± 1.94 Mg/ha, non-irrigated: 3.10 ± 0.47 Mg/ha). This suggests that flood irrigation enhanced growth; however, the difference in productivity between the control and irrigated plots was apparent already in early May 1999, i.e. 3 months before the irrigation was applied. At that time, the density and biomass of newly formed shoots was much higher in the plot that was later irrigated than in the non-irrigated plot. The biomass of newly emerged shoots, which were measured separately, was 130 ± 73 g/m^2 in the later irrigated and 9.7 ± 7.9 g/m^2 in the non-irrigated plot.

In the following year, no effect on growth was apparent: Dry mass increment of shoots that were marked in April 2000 and measured again in April 2001 was similar in the previously irrigated and the non-irrigated subplots (Table 7).

Effects of use

Alhagi

The 'use' treatments (control, reduced use, use) were applied in late August 1999. In August 2000, biomass densities of the three use treatments within the non-irrigated plot were not significantly different (Table 2), suggesting that different use had no effect. However, in summer 1999, before the use treatments were applied, biomass densities had been higher in the 'reduced use' and 'use' treatments than in the 'no use' treatment, and for the 'reduced use' treatment this difference was significant (Table 2). When compared to these 1999 values, production in 2000 had decreased significantly in the 'use' and 'reduced use' treatments, but had not changed significantly in the control, suggesting that both 'reduced use' and use in the local manner decreased production.

In the previously flood-irrigated plot, the same pattern as in the non-irrigated plot is indicated by the statistical analysis, with no significant decrease of production between years for the 'no use' subplot and significant decreases for the 'use' and 'reduced use' treatments (Table 2), suggesting a negative effect of the use treatment. However, the decrease in production between years was large in the 'no use' subplot, even if a paired *t*-test with Bonferroni correction indicated no significant difference.

Calligonum

Growth of marked shoots of *Calligonum* responded positively to the use treatment (removal of half of the biomass) applied in summer 1999 (Table 6). Even if both absolute and relative biomass increment do not significantly differ between 'use' and 'no use' treatments in 2000, the effect of thinning becomes apparent when comparing growth between the 2 study years: in the non-used subplots (both non-irrigated and previously irrigated), there was significantly less growth in 2000 than in 1999. In the used plots, on the other hand, relative biomass increment remained the same as in the year before in both non-irrigated and pre-

viously irrigated plot. Enhanced growth due to thinning apparently counterbalanced an overall trend for lower productivity in 2000.

Populus
After removal of nearly half the trees in October 1999, radial growth of remaining trees in the thinned stands in 2000 was significantly higher than that of trees in the non-thinned stands (Table 5). Production in the thinned subplots was 16.3% of the initial biomass in the 'use' subplots and 14.3% in the non-used subplots (irrigation treatments pooled).

Tamarix
Thinning strongly enhanced productivity of remaining shoots both in the non-irrigated and the previously irrigated plot. Relative basal area increment and relative dry mass increment of shoots in thinned stands in summer 2000 was more than two times higher than that of control plots (Table 7). In the previously irrigated plots, the difference in relative basal area increment between non-used and used subplots was significant, while the difference in absolute basal area increment was not, indicating that the distribution of shoot diameters was different between non-used and used subplots.

Discussion

Allometric relationships

The tight correlations between shoot cross-sectional area (or, in the case of *Alhagi*, shrub volume) and various biomass fractions shows that the established allometric equations are useful tools and lends credibility to the indirect biomass and production estimates. Close agreement of the regressions between basal area and biomass (*Calligonum*, *Tamarix* and *Populus*) with theoretical predictions based on hydrodynamic and mechanical requirements for shoot architecture (West et al. 1999) raises these allometric relationships from a purely empirical to a mechanistic level and in the case of the desert vegetation studied here suggests that architectures of these plants are to a high degree optimized for water transport, which seems a logical consequence of the high evaporative demand in their environment.

The close correlation between vertically projected shrub area of *Alhagi* (calculated as the area of a circle with the mean of shrub length and width as diameter) and shrub dry mass is encouraging and will be used for GIS-based automated determination of shrub mass from aerial photographs. This is an additional advantage of this type of regression equation over biomass estimates from basal area.

Biomass and production in relation to available water

Proceeding from assumptions implicit in previous research on Qira oasis (Xia et al. 1993), it was thought that all four species depend on natural or artificial flooding for their water supply in the foreland of the oasis. Natural (and artificial) floods occur quite late in the growing season, as water load in the river peaks in July and August. In *Calligonum*, *Populus* and *Tamarix*, the experimental flood irrigation was carried out during a phase of high water load of the river at the end of July/beginning of August; in *Alhagi* the irrigation was applied one month earlier, using groundwater pumped from a nearby well. It was expected that all species experience marked drought stress by then. Therefore, immediate effects of irrigation on plant water status were expected. Effects on growth of plants, on the other hand, were expected for the following growing season, for the treatment was applied too late in the growing season to clearly affect growth in the same year. It was thought that irrigation water would be stored in the soil and could be used by the vegetation for a prolonged period after the flood irrigation.

Considering the presumed dependence on flood irrigation as well as the fact that without irrigation there was no plant-available water in the entire soil profile above the capillary fringe of the groundwater (Thomas et al. 2000a), it was surprising that plants in the non-irrigated plots were healthy green and vigorous throughout the growing season (and in the irrigated plots before the irrigation). It was even more surprising that biomass density and production with or without flood irrigation were quite high compared to other shrub deserts (Whittaker and Likens 1975; Whittaker and Niering 1975) and were in the lower range of mesic vegetation Ellenberg et al. 1986).

It is clear that an annual production of up to 11.3 Mg/ha in the non-irrigated plots cannot be supported by 35 mm of water, which is the average annual sum of precipitation in that area. Precipitation was not measured in 1999 and 2000, but it was observed on site that it was negligible during both growing seasons (A. Foetzki, personal observation) and can be ruled out as a source of water for the vegetation. Even if these plants had an unusually high water use efficiency of production and were theoretically able to produce up to 11 Mg/ha of aboveground biomass (plus a corresponding amount of belowground biomass) from 35 mm of water, it is not clear how they could make use of the rare rainfall because there were virtually no fine roots in the topsoil.

The only plausible explanation for the high biomass production is that all four species have direct access to groundwater or at least the capillary fringe above the groundwater table. In the spring, groundwater is at a depth of 12–16 m underneath the *Alhagi* stand, at 3.6 m in the irrigated *Populus* stand, at 5.7–12 m in *Tamarix* (but later we also observed vigorously growing *Tamarix* stands at 22 m depth to groundwater), and at deeper than 7.5 m in *Calligonum*. These are not unusual depths for phreatophytic plants (Canadell et al. 1996; Jackson et al. 1996). In particular, *Alhagi* is able to tap into a water table up to 15 m below the soil surface Kerr 1963; Kerr et al. 1965)

Permanent access to groundwater would explain the high production in a virtually dry soil in a region that is practically without precipitation. This situation is not uncommon in deserts. For example, *Haloxylon ammodendron* (= *aphyllum*, black saxaul), a 5–9 m high tree, occurs at 5–8 m distance to groundwater in the Karakum desert (Turkmenistan). High productivity of this species (aboveground biomass: 5.2 Mg/ha. aboveground production: 1.2 Mg/ha) is made possible only by water uptake from groundwater (Walter and Breckle 1999). These values are comparable to those reported here.

Permanent access to groundwater would also explain why there was no clear beneficial effect of the experimental flood irrigation (see discussion below). Vegetation adapted to seasonal water input into the soil from rain or floods probably would have responded much differently. Another factor that may contribute to the lack of an effect of flooding and has to be considered in this context is soil texture – silt soils have high sorption capacity for water, but low infiltration and transport rates. In a sandy soil, water from a flood irrigation would get to the roots much faster than in this silt-dominated, non-aggregated soil, where it took several weeks for the flooding water to reach a significant depth in the soil profile (Thomas et al. 2000a). Besides the low precipitation, this is probably one reason why there are no annual species in the foreland – this vegetation is not adjusted to precipitation, as there is virtually none, but even if there was some, it would not easily enter the soil.

If deep groundwater is the sole water source, then how could this vegetation establish, and (how) does it regenerate? According to Jäkel and Hofmann (1991), Tian (1991) and to our personal observations of 4 years, virtually the only window of opportunity for recruitment of new individuals from seed opens when flooding events, which happen in the form of torrentially streaming masses of water and silt and are accompanied by shifts of river beds of several hundred meters, remove several meters of soil in a given place, creating lowland areas close to groundwater, where seeds can germinate and reach the groundwater table before the top soil dries out and before the soil surface rises again by accumulation of windblown silt (we recorded average accumulation rates of up to 7.5 cm per year).

As more and more reservoirs are built in the mountains upstream for storing the summer floodwaters until they are needed again for irrigation of fields in spring, such flooding events will become less frequent in the foreland and this will further reduce natural regeneration of the protective vegetation.

The pattern that normal conditions allow survival of established vegetation, but regeneration of this vegetation requires special conditions that rarely occur, is also seen in other ecosystems. However, in contrast to e.g. semi-arid zones of Peru and Chile, where temporary increases in precipitation due to El Niño events induce regeneration of woody species (Holmgren et al. 2001), precipitation at the southern fringe of the Taklamakan is normally not even sufficient to induce germination, and never sufficient to support plants or ensure that roots reach groundwater. If however El Niño Southern Oscillation events cause increased

precipitation in the mountains upstream, which seems possible based on information provided by Allan et al. (1996), then the intensity of summer floods could increase in such years. At least under natural conditions, the probability of plant establishment in lowland areas newly exposed by shifting rivers would increase. Efforts are under way to obtain data on stream and aquifer flow rates in order to assess possible relationships with tree ring data for *P. euphratica* and *T. ramosissima*.

This vegetation's dependence on groundwater has important implications for its further existence, as the use of groundwater for irrigation in the oasis has greatly increased in recent years. The number of wells in the oasis has gone up from 23 to 89 since 1997, and drilling of more wells is planned. According to local information, the groundwater table within the oasis seasonally fluctuates with an amplitude of 4 m. The annual course of this fluctuation is such that beginning in spring, groundwater levels steadily decrease due to pumping of groundwater for field irrigation, until summer floods arrive and river water can be used for irrigation. From then on it takes until the next spring for groundwater to regain its initial level. It is not clear how far these fluctuations extend into the foreland, or how much the foreland vegetation is affected by them. Local authorities are aware of the fact that groundwater is a limited resource but do not yet take into account that the protective foreland vegetation also needs groundwater. In each case, a further lowering of the groundwater level and excessive fluctuations of groundwater must be prevented in order to maintain the foreland vegetation.

Effects of flood irrigation

Contrary to the hypothesis, flood irrigation did not increase soil water content sufficiently to enable water uptake by roots (Thomas et al. 2000a). According to a yet unpublished pF curve for this soil, volumetric water contents between 10 and 15% correspond to soil water potentials of approx. −100 to −10 MPa, which are too low to allow water uptake by plant roots. Only in the uppermost soil layers did the water content for a short time exceed those values; there, however, virtually no fine roots of any of the target species were found. It took several weeks for the water to reach a depth of 2 m, and there, water content was increased only by a few percent. Hence, the soil's pore size distribution is very unfavorable for rapid water transport due to the lack of aggregation and the high silt fraction. As a consequence, flooding did not noticeably recharge the ground water.

The lack of a flooding effect in *Calligonum* is not surprising; there were no fine roots in the soil down to the depth to which flooding water penetrated, and vertical water transport was very slow (Thomas et al. 2000). It took almost 2 weeks for the soil water content at 0.25 m depth to increase to 7% after the flooding, which according to this soil's pF characteristic is equivalent to a soil water potential of −100 MPa (unpublished data). Soil water content at 1 m depth never exceeded 5%.

Yet, flood irrigation seemed to have enhanced growth of *Populus* and *Tamarix*, judging by the difference in production between the non-irrigated and the irrigated plot; however several observations make it difficult to explain how this could have been accomplished. First of all, the irrigation treatments were applied very late in the growing season. In *Populus* trunk diameter growth and thus biomass accumulation had already ceased. Even if we assume that biomass accumulation continued after the irrigation and was stimulated by the additional water supply, it could not account for the two to three times higher production in the irrigated *Populus* stand and the large differences in *Tamarix* biomass production. Second, very few fine roots of both species were found in the soil depths to which substantial amounts of irrigation water infiltrated, but many live fine roots were found in the capillary fringe of the groundwater. In this respect the root system structure of both species is very different from that of forests that rely on rain for their water supply or of orchard trees that are regularly irrigated, indicating that precipitation or flooding do not normally contribute to water supply of this vegetation. Third, plants looked green and vigorous throughout the growing season, did not experience severe drought stress before or after the flooding (Thomas et al. 2000b) and predawn leaf water potential was not affected by the flood irrigation treatment (Foetzki 2003).

Still, the difference in production between the non-irrigated and the irrigated *Populus* and *Tamarix* plots need an explanation. *Populus* trees in the non-irrigated plot were thinner than in the

irrigated plot (median diameter of non-irrigated trees: 6.53 cm; irrigated trees: 7.8 cm), even though both stands were 22 years old, as was confirmed by tree ring counts. This suggests a general difference in productivity between the two stands, though not of the magnitude observed in the growing season 1999. There is no obvious reason that would explain this difference. Soils were uniform and leaf nutrient status was similar. Both stands were completely defoliated at least once during the spring of 1999 due to mass propagation of two unknown species of caterpillars. It may be that the non-irrigated stand was affected more severely than the stand that was to be irrigated and that this increased the difference in productivity. Also, groundwater levels in the control and irrigated plots could be different, or the magnitude of their fluctuations, and that in turn could influence growth rate. $\delta^{13}C$ values point in that direction because they were significantly lower (more negative) in the irrigated than in the non-irrigated plot throughout the growing season, i.e. several months before the irrigation, and were unaffected by the irrigation (Foetzki 2003). Depth and fluctuations of the groundwater table in these sites as well as the question whether growth rate of *Populus* depends on groundwater depth need further study. A recent finding points into a completely different direction: it was discovered that all trees on the irrigated plot except one are genetically identical (H. Bruelheide, unpublished data). It is probable that a genetically different clone grows in the non-irrigated plot, which is several hundred meters away, and it could be that that clone is in some respect less efficient, which would explain the lower productivity on the non-irrigated plot.

As in *Populus*, there seems to be a general difference in productivity between the two *Tamarix* plots. Already in April 1999 the number of new shoots in the irrigated plot was twice as high as in the non-irrigated plot, and the biomass of these new shoots at that time was six times higher in the irrigated plot. The non-irrigated plot was established on a several meters high dune to prevent accidental flooding, and the plot that was to be irrigated was established in the plain adjoining the dune to facilitate experimental flooding. We suspect that the difference in distance to groundwater between the non-irrigated and the irrigated plot could be responsible for the difference in productivity. This was confirmed by carbon stable isotope data, because, as for *Populus*, $\delta^{13}C$ values were significantly lower (more negative) in the irrigated than in the non-irrigated plot throughout the growing season, i.e. several months before the irrigation, and were unaffected by the irrigation (Foetzki 2003). The question whether depth of the groundwater table affects productivity of *Tamarix* and *Populus* is presently being addressed in a separate study.

The negative response to irrigation of *Alhagi* can be explained by competition from the thick, continuous layer of annual species that had rapidly developed after flooding. These plants nearly doubled *Alhagi* in fresh mass and successfully competed for light with the *Alhagi* shrubs. Their growth was supported by irrigation water in the uppermost soil horizon for several months. No such effect was observed in any of the other sites. Their presence in the seed bank at the *Alhagi* site further supports the idea that this area is abandoned farmland. Though these annual species were only a transient element of the vegetation, they probably also indirectly affected growth of *Alhagi* in the next year, in which biomass was even lower than in the previous year. Lower production was not only due to lower shrub mass, but also to a significant decrease in shrub density, which may have been caused by belowground herbivory. It was observed that burrows of rodent-like animals of an unknown species that are thought to feed on and destroy belowground plant parts of *Alhagi* were much more frequent on that plot. We assume that these animals were probably attracted by the moisture in the uppermost soil layer and by the shelter, the favorable microclimate as well as the ample supply of fresh plant tissue and seeds provided by the dense vegetation.

Effects of use

Thinning enhanced growth of remaining shoots – this was clearly visible in *Tamarix*, *Populus* and, indirectly but nonetheless clearly, in *Calligonum*. Higher transpiration rates per unit leaf area were observed in thinned stands of *Tamarix* and *Populus* than in non-thinned stands (A. Foetzki, unpublished data), suggesting that the positive effect of thinning is at least in part due to a better water supply for the remaining shoots or trees.

This is somewhat unexpected, because if all plants are rooted in the groundwater or the capillary fringe, water is not really a limiting resource. However, one explanation is that hydraulic resistance of the root system of these clonally growing species limits water flux, and after thinning theoretically this limitation should be less severe, as only half the water flux is required. Thinning may also increase photosynthetic carbon gain of remaining shoots by improved light penetration into the canopy of dense *Tamarix* shrubs. Additionally, the positive effect of thinning may be explained by the fact that after thinning the remaining ramets have a quantity of root-stored carbon at their disposal that once had to suffice for twice the number of shoots. On the other hand, the remaining shoots had to supply more root biomass with carbon. This was apparently no problem in the first year after thinning, when previously stored carbon could be used, but may be a problem later and may eventually lead to an alleviation of the positive effect of thinning.

In *Alhagi*, the use treatments (complete harvests) were applied in late August 1999 and effects on production in the following growing season were expected. Only effects of use on growth in the non-irrigated treatments are considered because growth in the irrigated plot was obviously disturbed by competition from annual species and probably also by increased herbivory by soil-burrowing rodents.

Before the treatment was applied, production was higher in the 'reduced use' and 'use' subplots than in the 'no use' subplot, and after the treatments were applied, production in the used subplots decreased significantly, while that of the 'no use' subplot did not. Thus, the use treatment had a negative effect on growth. Probably, harvesting *Alhagi* in the end of August prevented recharging of belowground storage organs that would otherwise have continued until the end of the growing season in October, and harvesting also prevented retranslocation of valuable N-organic compounds from aboveground parts to the perennial belowground compartment, thus rendering the plants with less resources for maintaining the extensive belowground system and for growing several sets of new shoots in spring, which according to our observation is necessary under the heavy grazing pressure that prevails both outside and inside the fence.

Different initial biomass densities in the three subplots reflect spatial variations of stand density that are probably due to different use histories. All experimental plots had been established in stands that were not cut the year before the experiment, judging by the large number of 1-year-old dead shrubs on all plots. Yet it is clear that the stands had been grazed regularly and had been cut at irregular intervals until 2 years before the experiment. If shrubs would not be removed by harvest for several years, we would find a thicket of dead, entangled *Alhagi* shrubs in different states of decay in these dense stands.

Qira oasis may serve as a model for other oases at the southern margin of the Taklamakan with respect to land use, water availability and the ecological and economical role of the foreland vegetation (Coque et al. 1991; Xia et al. 1993). The vegetation is poorer in species, but otherwise very similar to that of other Central Asian deserts Walter and Box 1983). Comparable ecological settings are found throughout Central Asia (Walter and Breckle 1999). Therefore, results are of significance for these regions as well.

Conclusions

The vegetation types studied occur in a very dry and arid climate, yet their biomass density and productivity is similar to that of mesic vegetation. The only plausible explanation for this is that they all have permanent access to groundwater and do not depend on precipitation or flooding for survival (but probably for regeneration).

In order to preserve this vegetation as a shelter against sand drift, as grazing land and as an important source of forage, fuel and construction material, groundwater must be protected and its present level must be preserved until its effect on the foreland vegetation is better known. The effects of increasing seasonal fluctuations or even a decrease in groundwater level on the foreland vegetation require further study. Any further increase of groundwater use for field irrigation in the oasis should be postponed until the effects of that use on the groundwater table in the foreland surrounding the oasis have been studied.

Thinning of the woody species enhances productivity of the remaining plant parts, which to a

limited extend compensates for the removal of biomass. High productivity and elasticity make a sustainable use of the foreland vegetation seem feasible if use is properly managed. This requires that harvest is quantitatively limited to the annual biomass increment and qualitatively limited to the removal of aboveground plant parts.

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