Investigating water problems of *F. albida* along the Kuiseb river, Namibia

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ABSTRACT

Concern is mounting over widespread mortalities of the conspicuous *F. albida* trees along the ephemeral rivers in Namibia. Causes underlying the mortalities of *F. albida* are the lowering of the water table, natural senescence and a lack of recruitment of young trees or a combination of all three. In this study seasonal water-use efficiency determined by stable carbon isotopes and water-stress estimates provides a measure of both water used by the plant and of the water-stress impact on plant performance. Size class structure and mortality of *F. albida* along the Kuiseb river was also determined. The results suggest that pumping and a reduced number and magnitude of floods are the main cause of *F. albida* mortality on the Kuiseb river. Plants are unable to cope with the lowering of the water table and smaller trees appear to be more vulnerable than older trees. Human interference in the water cycle of the Kuiseb river and natural senescence appears to be driving the population dynamics of *F. albida*. In the absence of remedial measures the recruitment of this economically important species will remain constrained.

INTRODUCTION

In Namibia *Faidherbia albida* (formerly *Acacia albida*; common name Ana tree) is a tree which is restricted to the ephemeral rivers which have a higher soil moisture content than the surrounding plains. These rivers run from east to west across the Namib Desert into the sea. In this environment, *F. albida* is an economically important tree for humans and animals. A decrease in the availability of these trees would mean a decrease of productivity in livestock and game alike, and would contribute to desertification. Along most of the ephemeral rivers in Namibia old *F.albida* individuals are dying (Ward and Breen, 1983). Concern about the mortality of *F. albida* is growing. The most frequently-cited reason for the mortality is the lowering of the water table in ephemeral rivers (Jacobson et al. 1995; Ward and Breen, 1983; Theron et al. 1985; Bate and Walker, 1993; Jacobson et. al. 1994). Water for domestic and livestock consumption is being pumped out of boreholes. Furthermore, the recharge of the aquifers is decreased by dams situated upstream (Jacobson et. al., 1995). The water table is,

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METHODS AND MATERIALS

Study species: *F. albida*

Faidherbia albida occurs only in Africa but has a wide distribution from southern Africa up along the Nile to the Negev desert in Israel. It is also very common in East Africa and in the Sahel (Wood, 1989). Compared to closely related acacias, *F. albida* has a unique feature in that it sheds its leaves in the wet season and bears leaves in the dry season (Walter and Stadelmann, 1974). Because it bears leaves in the dry season it is an important fodder source during winter. *F. albida* is considered to have a high economic value. Throughout Africa the pods and leaves of *F. albida* are consumed by livestock and game. The seed pods are particularly valuable, with a high protein content (Unruh, 1993). They also contribute nitrogen to the soil from their symbiotic N_2 fixation relationship with bacteria (Dupuy and Dreyfus, 1992).

F. albida is well adapted to an ephemeral river environment. It has a sprouting habit and tends to form clumps of trees which help them to withstand the force of the flood waters (Jacobson et al. 1995). A long tap root with lateral roots near the surface secures a groundwater source for the tree (Wood, 1989). Their seed dispersal mechanism is also adapted to the river environment. The water carries the pods of *F. albida* downstream where they can germinate. After a flood event many seedlings germinate, although most of them do not survive a year (Jacobson et al. 1995). Root growth at the seedling stage of *F. albida* is rapid. The root has to reach a stage where it can provide adequate moisture to the plant before the shoot develops (Wood, 1989). Seedling establishment depends solely on the water availability although some maybe eaten or trampled by goats. *F. albida* trees need big flood events to establish (Jacobson et al. 1995) so that enough soil water is available until the roots of the seedlings reach the ground water. These floods are infrequent; the last major flood on the Kuiseb occurred in 1972 (Fig. 2).

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therefore, steadily dropping. The trees cannot reach the water and therefore die from water stress. Ward and Breen (1983) hypothesised that younger *F. albida* trees have more flexible roots and can grow along with the dropping water table. Older trees, on the other hand, are reported to have inflexible roots and die once the water table sinks. Another possible cause of the high apparent total mortality in *F. albida* populations is natural senescence combined with a lack of recruitment. Senescence in any population is not problematic as long as there are young individuals to replace dying, older individuals. It appears that recruitment in *F. albida* population is rare, and that young trees establish during abnormally high flood periods. These floods are now infrequent because the dams further upstream have restricted water flow.

The extent of the water problems of *F. albida* were investigated along the Kuiseb river at borehole sites and non-borehole sites. I predicted that *F. albida* suffer higher water stress near boreholes than plants further away from pumping stations. I hypothesize that the lowered water table caused the mortality of *F. albida*, especially of larger trees. To test this hypothesis, stable carbon isotopes were used to determine long-term water-use efficiency (WUE) of *F. albida*. There is a relationship between the WUE and the $\delta^{13}C$ of the leaves of plants (see Methods). Martin and Thorestenson (1988) showed that variation in $\delta^{13}C$ in tomato leaves could explain 57 to 65% of the variability in whole plant WUE. Le Roux et al. (1996) found a weaker relationships between whole plant WUE and $\delta^{13}C$ of clones of *Eucalyptus grandis*. The variation in $\delta^{13}C$ value is therefore not always explained solely by the WUE of the whole plant. The $\delta^{13}C$ in C_3 plants is affected by environmental conditions and is also under some genetic control (Farquhar, 1989). In the Arizona desert the $\delta^{13}C$ of plant species appear to be mainly affected by the water availability. They have a higher WUE or lower $\delta^{13}C$ value as the soil water availability increases (Ehleringer and Cooper, 1988; Ehleringer, 1989; Ehleringer, 1993). Rundel and Sharifi (1993) also found that the desert shrub *L. tridentata* has the ability to change its WUE with water availability. This natural abundance technique was used to investigate the water problems of *F. albida* with the expectations of higher WUE at pumping stations and lower WUE far away. In addition to the carbon isotope study, water potentials were measured. The size class structure and the extent of the mortality of *F. albida* was determined to test the senescence hypothesis for declining *F. albida* numbers.
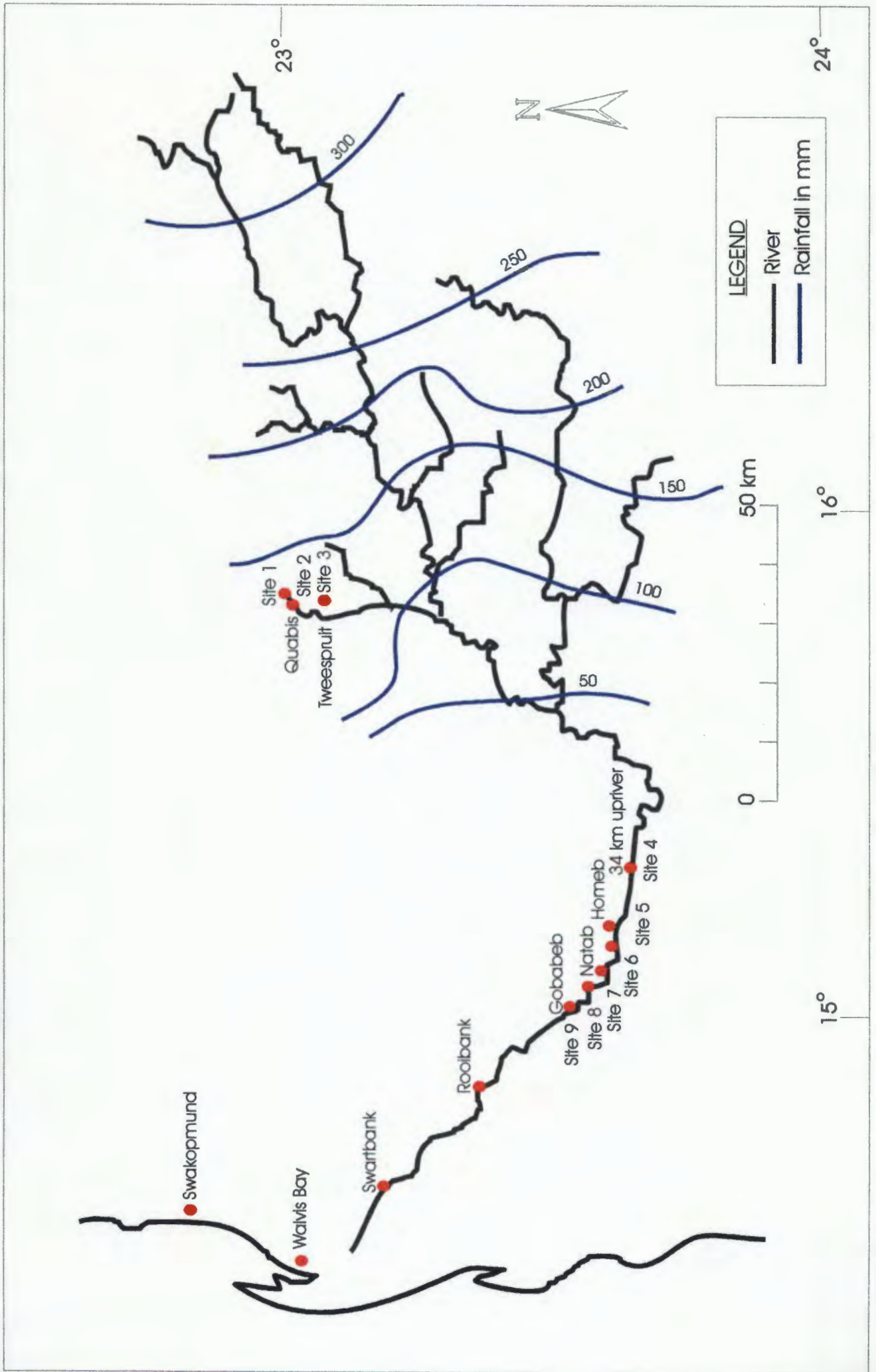
Fig. 1. A map of the Kuiseb river showing the locations of the study sites. Adapted from Jacobson et.al. 1995 and Van den Eynden et al. 1992.

Study area

The Kuiseb River is a linear oasis in the central Namib Desert which supports a diverse plant life (Fig. 1). This ephemeral river runs from the Khomas Hochland near Windhoek, through the Namib Desert into the sea near Walvis Bay. In the last 146 years the floods from the Kuiseb have reached the Atlantic on only 15 occasions; the last recorded occurrence was in 1963 (Theron et al. 1985). Although the river seldom reaches the sea, the water flooding from the mountains during summer is strong enough to prevent the sandy dune field which stretches from Lüdertizbucht to the Kuiseb from spreading north. The Kuiseb river is thus the border between the dunes and the gravel plains. Rain collects in the Kuiseb catchment and its tributaries to form run-off. It is this run-off water that is trapped and retained in farm dams and it may also seep through sand and permeable rock formations to recharge the underground water resources. Although the river only runs a few days a year (Fig. 2), large quantities of water flow in the sand aquifers of the river bed. Most run-off is contributed by the upper Kuiseb from the plateau and the escarpment with their well defined drainage systems (Fig.1). The lower Kuiseb in the desert is therefore dependent on the run-off originating in the Khomas Hochland for the recharge of its alluvial aquifers. This groundwater stored within alluvial deposits is an important supply to the riparian forests (Robinson, 1976). Aquifer water is also a critical source of water for the towns of Walvis Bay, Swakopmund, Arandis and Rössing Mine. To supply these growing towns with water, the water is pumped from the Kuiseb aquifers and the water table is steadily dropping. The recharge of flood water and rain is less than the increasing demand of the human settlements (Fig. 3). This decreasing water table may affect the riverine vegetation of the lower Kuiseb and cause trees such as *F.albida* to suffer water stress.
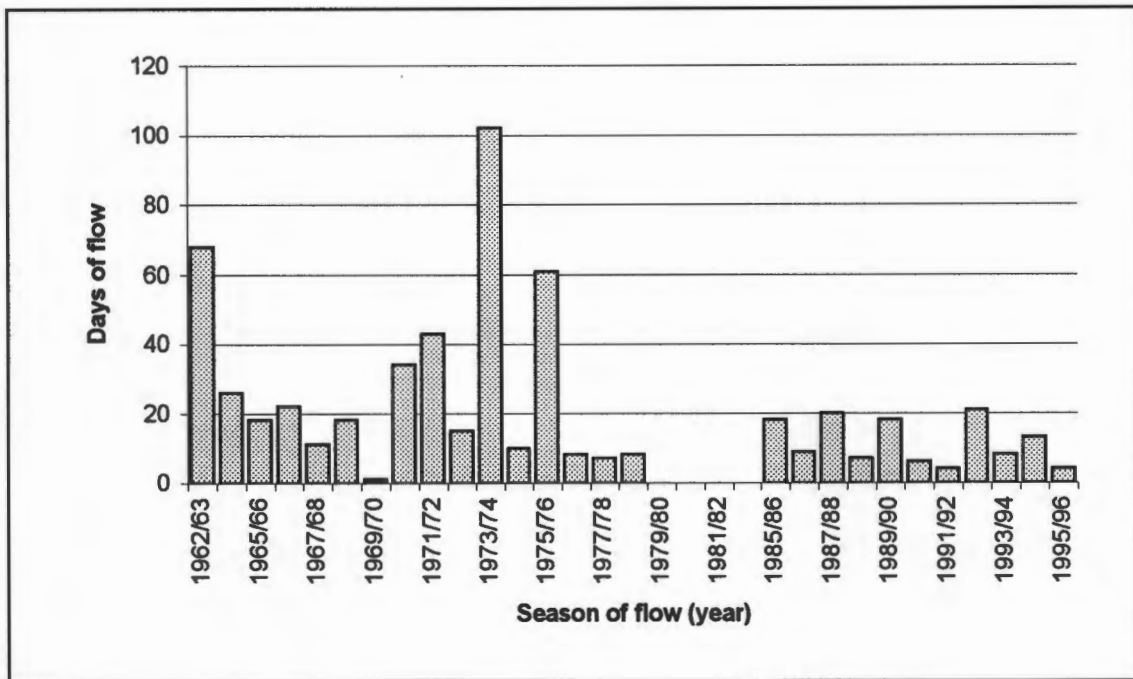
Fig. 2. Bar graph of the flood history of the lower Kuiseb River at Gobabeb (after Ward and Breen, 1983 and data from the Department of Environment and Tourism, Gobabeb)
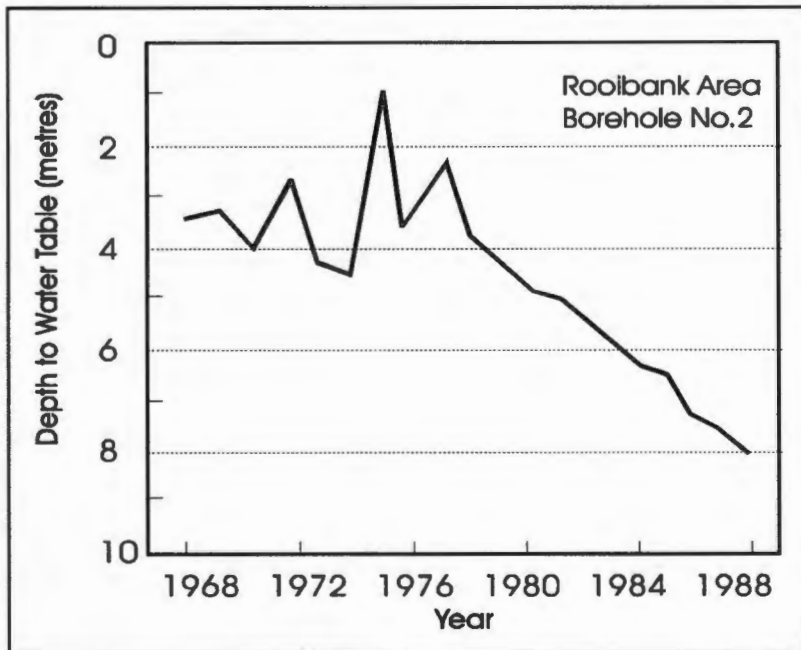

Fig. 3. The declining water table at the Rooibank pumping station on the lower Kuiseb river. From Jacobson et. al. 1995.

The four main plant species of the vegetation along the lower Kuiseb are *Faidherbia albida* which lines the active channel while *Acacia erioloba* (camel thorn), *Tamarix usneoides* and *Salvadora persica* occur on the flood plain. Further upriver and in the tributaries of the Kuiseb river other *Acacias* occurred such as *Acacia senegal, A. tortillis, A. karoo* and *A. erubescens*. The *F. albida* populations studied here were on the Kuiseb and the Nausgomab rivers, a tributary of the Kuiseb (Fig. 1). The sites on the Kuiseb were: 34 km upriver from Gobabeb (Site 4), Homeb (Site 5), midway between Homeb and Natab (Site 6), Natab (Site 7), between Natab and Gobabeb (Site 8), and Gobabeb (Site 9) (Fig. 1). At sites adjacent to a Topnaar village (Homeb, Natab and Gobabeb) a pumping station was present. On the Nausgomab river *F. albida* populations were on the farms Quabis and Tweespruit. These farms are at the edge of the Khomas Hochland on the eastern margin of the Namib Desert (Fig. 1). At Quabis only two sites were selected; one near a borehole and farmhouse (Site 2) and one upriver away from any pumping station (Site 1). The site at Tweespruit was adjacent to the farmhouse and a pumping station (Site 3). Site 1 on the farm Quabis is furthest upriver in the Kuiseb tributary while Site 9 (Gobabeb) is nearest to the sea (Fig. 1).

Table 1. Information about the boreholes where sampling took place. From the Department of Environment and Tourism (Gobabeb) and pers. comm. Captain Kooitjie, Mr Benefeld and W. van Rooyen.

Site	Depth of borehole	Water table	Water extraction
Quabis (Site 1)	5		$2m^3h^{-1}$
Quabis-upriver	60		$2m^3h^{-1}$
Tweespruit (Site 3)	101		$525m^3 mth^{-1}$
Gobabeb (Site 9)	20	14	$434m^3 mth^{-1}$
Natab (Site 7)	16	3	$110 m^3mth^{-1}$
Homeb (Site 5)	35		$110 m^3 mth^{-1}$

Distribution and mortality of *F. albida* along the Kuiseb River

To investigate the extent of mortality of *F. albida* I conducted a survey along the banks of the Kuiseb River. At sites 4 (34 km upriver), 5 (Homeb) and 9 (Gobabeb) I measured stem diameter and the percentage of dead material in the canopy of 50 consecutive trees. At Gobabeb and 34km upriver a further 30 trees on the flood plains were measured.

The percentage of dead material in the canopy was then used to draw up class distributions for all sites. To test for the difference in general shape of the class distributions a Kolmogorov-Smirnov test was used. This test is used to differentiate between the size-class distributions at the different sites. To determine whether more small trees (stem diameter < 30cm) than big trees (stem diameter > 30cm) are dying a Kolmogorov-Smirnov analysis was also used. It was arbitrarily decided to take 30cm as the cut-off between large and small trees.

The stem diameter was used to draw up a size class distribution of *F. albida* along the Kuiseb river. Stem diameter of the trees was grouped into 10cm size classes to determine regeneration gaps and age structure (Walker et al. 1977). Tree diameter of *F.albida* is positively correlated with the tree size and can therefore be used to distinguish between small and large *F. albida*. To test for differences in the size class distribution between the sites a Kolmogorov-Smirnov analysis was performed.

Water potential measurements

Plant water potential was measured to assess the water status of *F. albida*. A decrease in water potential of a plant indicates water stress and plant water potentials exhibit diurnal fluctuations because transpiration increases faster than water uptake during the first part of each day. On sunny days, water potential values of leaves are maximal at sunrise and minimal during the afternoon (Walter and Stadelmann, 1974). By measuring water potentials at pre-dawn and midday the difference in the water potential can be determined. The higher the difference the less water the plant has available to compensate for transpirational losses. The

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pressure-bomb technique (Pearcy et al., 1989) was used to determine the water potentials (xylem pressure potentials; XPP) of *F.albida* at dawn and noon.

The pressure-bomb technique is used as a measure of plant water status. Twigs were cut from the plants and placed in a pressure chamber (PMS Scholander bomb) with the cut end projecting through the hole in a rubber bung. The pressure was increased until water in the xylem had wet the whole surface of the cut twig and the balancing pressure in the chamber was read off from the gauge (Pearcy et. al., 1989). Water potential measurements were undertaken on two sites on the Kuiseb and two sites on the Nausgomab river. The sites on the Kuiseb river were at 34 km upriver (Site 4) and at Gobabeb (Site 9) where a pumping station is present. On the Nausgomab river, measurements were taken at the Quabis farmhouse (Site 2) and further upriver away from the pumping station (Site 1). Ten trees of varying sizes were selected to measure the leaf water potential at dawn and at midday. Material from the same side of a tree was used for both measurements so as to allow for possible aspect differences.

A nested ANCOVA analysis was performed to test for differences between the Kuiseb and Nausgomab river and for position away from boreholes. The $\log_{10}$ tree diameter taken as $\log_{10}$ was used as the covariate to control for any possible differences due to tree size. The multiple regression for $\log_{10}$ difference in water potential between midday and pre-dawn or water potential at midday against $\log_{10}$ tree diameter was calculated. This was done for each site individually and all sites lumped together.

Carbon isotopes to determine water-use efficiency

Seasonal water-use efficiency determined by stable carbon isotopes provides a measure of both water used by the plant and the water stress impact on the plant. Water-use efficiency (WUE) is the plant's transpiration efficiency - the ratio of dry matter produced to water used. Using carbon isotopes gives a photosynthetic WUE over the entire life cycle (Lauteri et. al. 1993) instead of instantaneous results such as would be obtained if an infrared gas analyzer (IRGA) had been used. WUE and $\delta^{13}C$ discrimination values are negatively correlated for C_3

species (Hubick and Gibson, 1993). This is because there is a linear relationship between $\delta^{13}C$ and the ratio of intercellular to atmospheric partial pressure of CO_2 (p_i/p_a) (Farquhar et al. 1982 cited by Lauteri et al. 1993). The formula for this relationship is: $\Delta\delta = (a + (b-a) p_i/p_a - d)$ where $\Delta\delta$ = change in discrimination value, a = discrimination by diffusion, b = discrimination by Rubisco, p_i = CO_2 internal pressure, p_a = CO_2 external pressure and d = discrimination by any mechanism (Farquhar et al. 1989).

Atmospheric CO_2 contains ^{12}C and ^{13}C in the ratio 99:1 (Farquhar et. al. 1989). Plants discriminate against $^{13}CO_2$ during photosynthetic carbon assimilation. In C_3 species this discrimination increases with an increase in the ratio of intercellular and atmospheric partial pressure of CO_2 (above cited relationship). The more water-use efficient a plant, the higher its $^{13}C/^{12}C$ ratio. A plant which is WUE will keep its stomata partially to fully closed and thereby lower its CO_2 concentration in the mesophyll cells. The enzyme which incorporates CO_2 into the Krebs cycle, Rubisco, is forced to incorporate ^{13}C and ^{12}C and cannot discriminate as much against ^{13}C. *F.albida* trees which are not as WUE and leave their stomata open will discrimination more against ^{13}C and have a lower $^{13}C/^{12}C$ ratio .

At all sites, leaves from 10 *F. albida* individually were collected and dried. The leaves were then ground (0.6 mm) to get a homogenous sample for isotope analysis. Leaf samples for mass spectrometer analysis were in the range of 0.05-0.08 mg. Carbon from the leaf dry matter is collected as carbon dioxide after combustion in CO_2 -free oxygen and removal of other oxidation products. $^{12}CO_2$ has a mass-to-charge ratio of 44 and $^{13}CO_2$ of 45. These mass ratios are then monitored in the mass spectrometer to obtain the $^{13}C/^{12}C$ ratio (Farquhar, 1988). There is, however , a contribution to the 45 mass ratio by $^{12}C^{17}O^{16}O$ which has to be corrected for. This isotopic carbon ratio between $^{13}CO_2$ and $^{12}CO_2$ was determined using an automated ^{13}C analyzer-mass spectrometer (Finnegan MAT 252; Bremen, Germany). The isotopic composition of the CO_2 of the leaf sample is expressed relative to the isotopic composition of the PDB standard. These deviations from the standard are written as $\delta^{13}C$ which is the ratio between $^{13}C/^{12}C$ and is expressed in per mil (‰).

A nested ANCOVA analysis was performed to test for differences between the Kuiseb and Nausgomab river using the $\delta^{13}C$ values of *F. albida*. The tree diameter was used as the

covariate to control for any possible differences due to tree size. A nested ANCOVA analysis was also used to test for differences in WUE of *F. albida* near and far away from a pumping station with the tree diameter as the covariate. The effect of tree size on the $\delta^{13}C$ was assessed with a regression and an independent t-test with small trees having a stem diameter less than 30cm and large trees greater than 30cm. A multiple regression analysis was performed testing the relationship of $\delta^{13}C$ to the distance upstream from Gobabeb and correlation coefficients were calculated to test for any relationships between the $\delta^{13}C$ values and the water potential measurements.

RESULTS

Size structure and mortality of *F. albida* along the Kuiseb river

Along the Kuiseb river, there are few young and many old *F. albida* trees (Fig. 4-6). In comparing the three sites (Site 4,5&9) along the Kuiseb, the size class distributions were different although not significantly so (Fig. 4-6). Only between the Homeb river channel and the Gobabeb flood plain was there a significant difference (p<0.01) in the shape of their size class distributions. None of the sites had a stable size structure of an expected negative exponential distribution (Walker et al. 1986), mainly because trees were absent from the first size class. Gobabeb had the highest recruitment of *F. albida* but very few large trees (Fig. 5). Homeb on the other hand had small trees missing up to the 60cm size class and a high number of trees in the large size classes (Fig. 6). All sites appear to have too few small trees and gaps in the larger sized trees.

Except for the 34 km upriver site none of the *F. albida* at the other sites had a very high percentage of intact canopy (Fig.7-9). The most similar sites, which also had the least damaged trees, were Site 4 on the riverbank and floodplain and Gobabeb (Site 9) on the riverbank (Table 2). At Gobabeb on the floodplain most of the *F. albida* are dead while near to the channel their survival is higher (Fig. 7). At Homeb 10% of the trees are dead and many have large parts of their canopy dying (Fig. 8). The 34km site (on the riverbank and
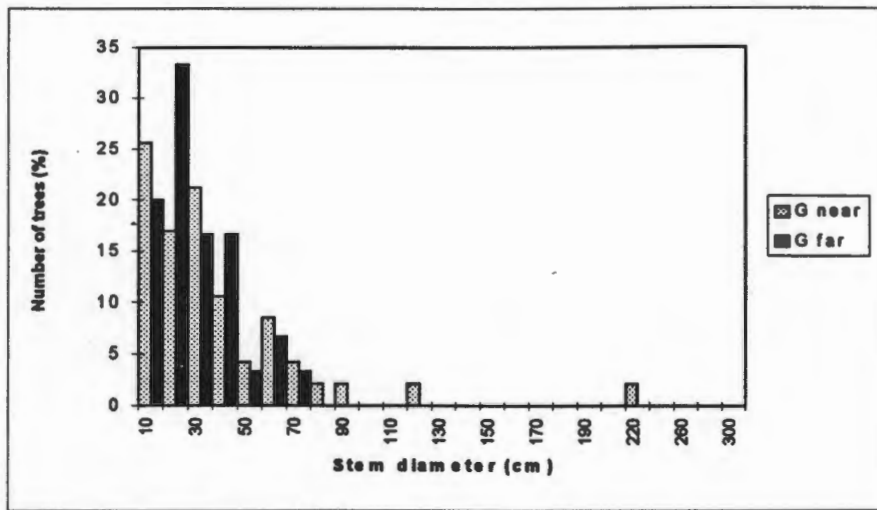
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Fig. 4. Size class distribution of *F. albida* at Gobabeb near the Kuiseb channel (G near)and on the flood plains (G far).
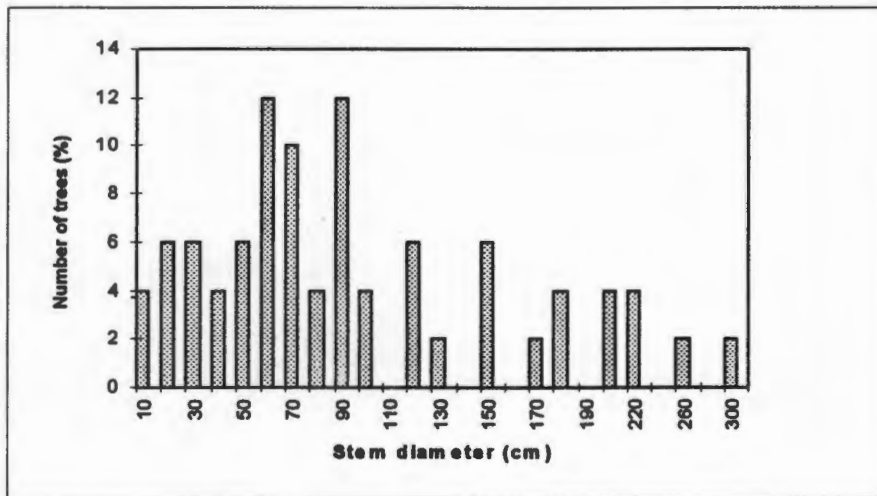

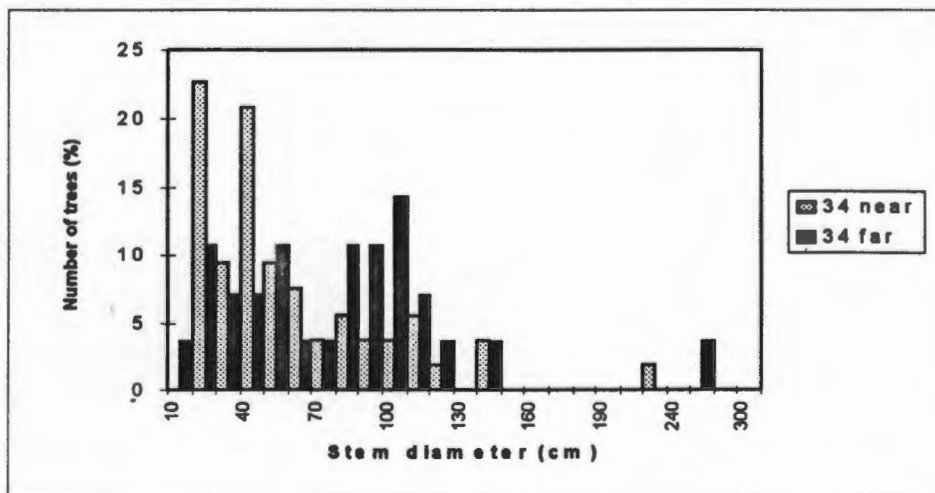**Fig. 5.** Size class distribution of *F. albida* at Homeb next to the Kuiseb channel

Fig. 6. Size class distribution of *F. albida* at 34 km upriver from Gobabeb next to the Kuiseb river channel (34 near) and on the flood plains (34 far).
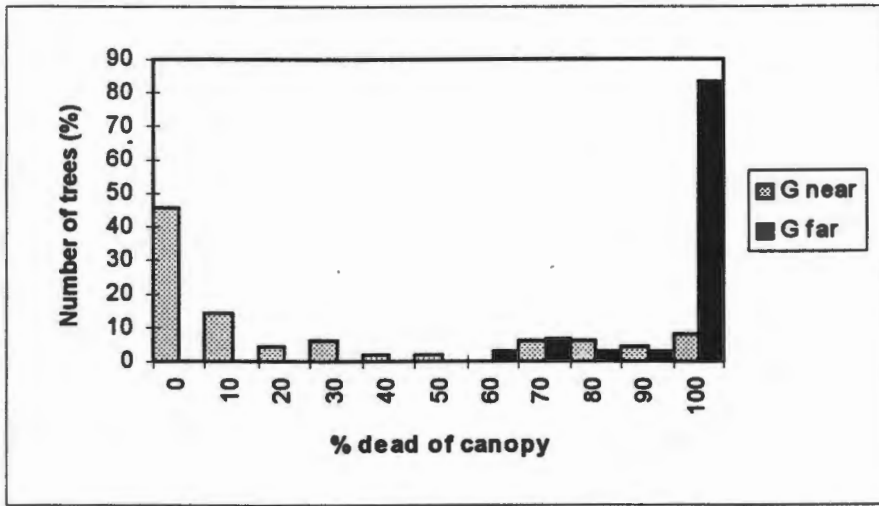
Fig. 7 . The class distribution of percentage dead material in the canopy of *F. albida* at Gobabeb next to the Kuiseb river channel (G near) and on the flood plain (G far).
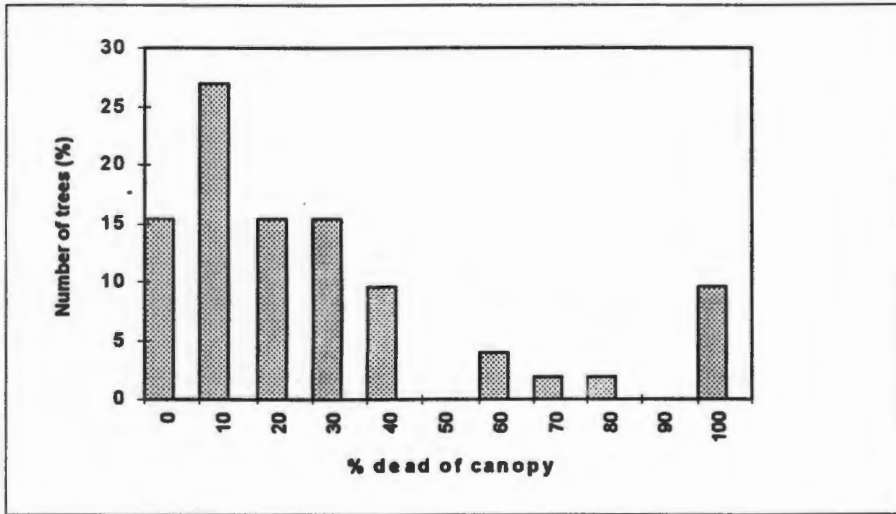

Fig. 8. The class distribution of percentage dead material in the canopy of *F. albida* at Homeb next to the Kuiseb river channel.
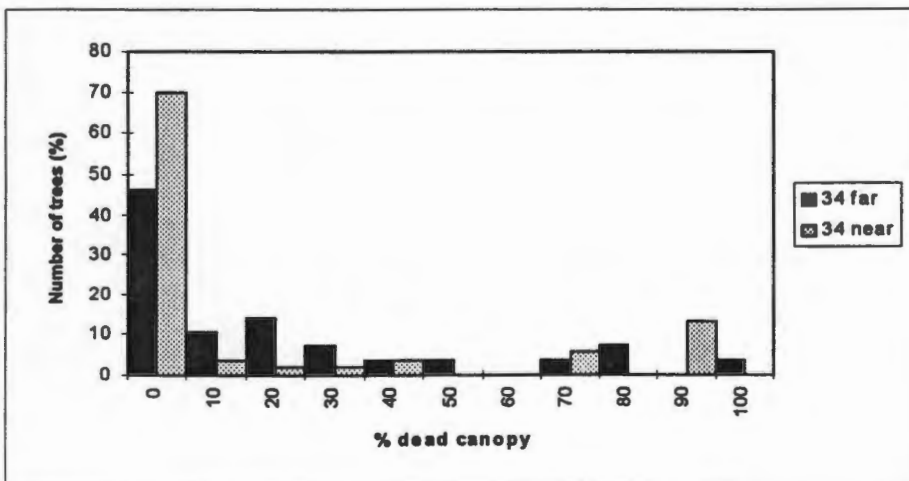

Fig. 9. The class distribution of percentage dead material in the canopy of *F. albida* at 34 km upriver from Gobabeb next to the Kuiseb river channel (34 near)and on the flood plains (34 far).

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floodplain) is not significantly different from Gobabeb on the riverbank (Table 2). If Gobabeb at the riverbank is therefore excluded the three positions on the Kuiseb river (34km upriver, Homeb and Gobabeb on the floodplain) are significantly different in their amount of dead material in the canopy (Table 2). Small and large trees have also significantly different percentages of their canopy dying ($p<0.001$). The smaller trees had on average 50 ± 44.37 % dead canopy while the older trees had only 22.15 ± 33.73 % dead canopy.

Table 2. Mean and standard deviation of percentage of dead canopy of *F. albida* at sites along the Kuiseb river. A Kolmogorov-Smirnov analysis was used to test for differences in the class distributions of percentage dead canopy between two sites.

SITES COMPARED	P-LEVEL	SITES	MEAN AND STD. DEV.
Gobabeb riverbank: Gobabeb floodplains	< 0.001	Gobabeb riverbank	26.70 ± 36.02
Gobabeb floodplain: 34 km floodplain	< 0.001	Gobabeb floodplain	95.67 ± 10.73
Homeb riverbank: Gobabeb riverbank	< 0.025	Homeb riverbank	28.37 ± 30.01
34 km riverbank: Gobabeb riverbank	> 0.10	34 km riverbank	21.70 ± 36.87
34 km floodplain: 34 km riverbank	> 0.10	34 km floodplain	20.00 ± 29.11
34 km riverbank: Homeb riverbank	< 0.001		

Water potential

F. albida seemed to be more water stressed further away from pumping stations than near them (Fig. 10&11). On both rivers the pre-dawn water potentials of the trees indicated that the trees were significantly less stressed near a borehole (Site 2&9) than far way (Site 1&4) (Fig. 10). At midday the Kuiseb upriver site (4) had the lowest water potential and the Nausgomab upriver site (1) showed high variability in water potentials (Fig. 11). This is also an indication of greater water stress at the upriver sites of the rivers. The ANCOVA gave a significant overall difference between sites close and far away from a borehole (Table 3). This was mainly due to a large difference at the Nausgomab river (Site 1&2) and not at the Kuiseb river (Site 4&8) which can be seen from the larger least square means of the borehole sites on the Nausgomab river (Table 4). There was a significant difference between the water potential

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of trees on the Nausgomab and the Kuiseb rivers (Table 3) with more negative midday water potentials occurring in the Kuiseb (Table 4). The midday and pre-dawn water potential difference was smaller on the Nausgomab than on the Kuiseb river (Table 4). The main difference between the Nausgomab and the Kuiseb river is contributed by Site 1 which showed high variability and a small midday/pre-dawn water potential difference. Sites 2, 4 & 9 showed similar trends in their midday and dawn water potentials (Fig. 10&11) with slightly lower values for the Kuiseb upriver site 4.

The regression relating water potential to tree size was not significant. There is no effect of tree size on water potential regardless of whether the sites were analysed separately or lumped together. There was also no difference between water potential at midday (F=1.49; P=0.23; error d.f.=38) or the water potential difference between midday and dawn (F=0.49; P=0.49; error d.f.=35) of different sized trees.
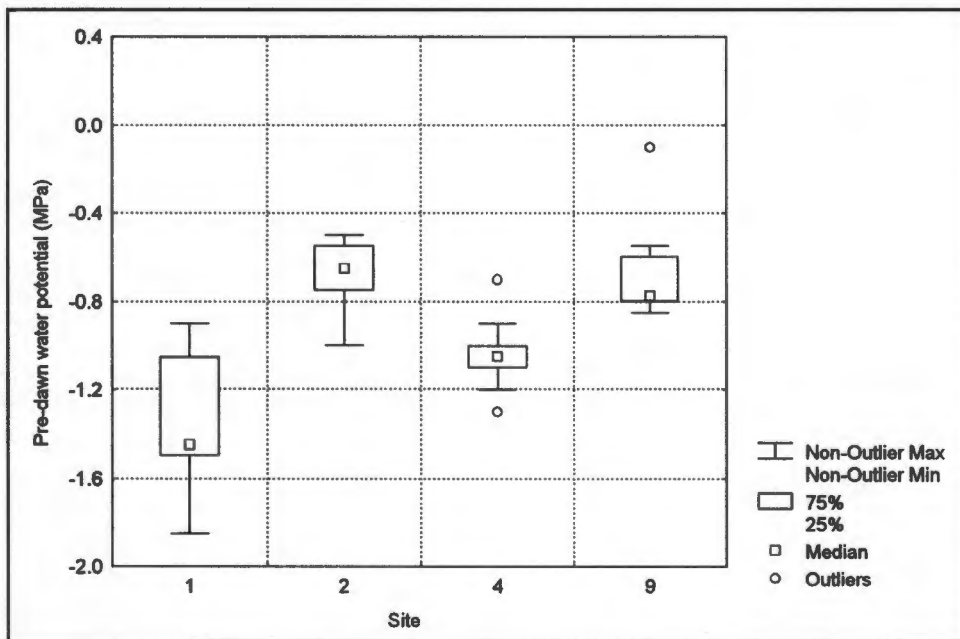

Fig. 10. The pre-dawn water potentials of *F. albida* summarized in box-and-whisker plots for the Nausgomab river, Site 1 (Quabis upriver) Site 2 (Quabis near borehole), and the Kuiseb river Site 4 (34 km upriver) and Site 9 (Gobabeb).
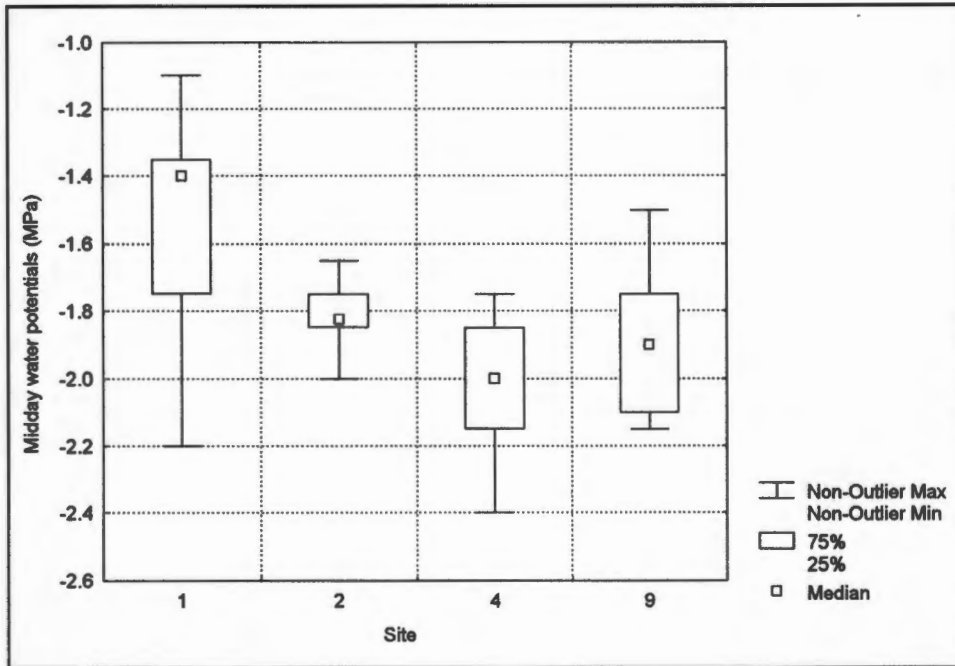
Fig. 11. The midday water potentials of *F. albida* summarized in a box-and-whisker plots for the Nausgomab (Sites 1&2) and the Kuiseb (Sites 4&9) rivers.

Table 3. ANCOVA analysis of water potentials of *F. albida* on the Kuiseb and Nausgomab river with $\log_{10}$ difference between midday and dawn water potential or $\log_{10}$ midday water potential as the dependent variable and $\log_{10}$ tree diameter as the covariate.

	Midday/ pre-dawn water potential difference	Midday water potential
	F-RATIO	**F-RATIO**
Tree diameter	0.24	2.82
Kuiseb/Nausgomab	26.70**	9.46*
Near/ far from borehole	31.92**	5.42*

* P < 0.05, ** P < 0.01, *** P < 0.001

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Table 4. Adjusted least square mean from an ANCOVA (covariate = $\log_{10}$ tree diameter) of negative water potential differences between midday and dawn, and midday water potentials of *F. albida*.

	Midday/ pre-dawn water potential difference	Midday water potential
	ADJ. LS MEAN ±STD. ERROR	**ADJ. LS MEAN ±STD. ERROR**
Nausgomab	0.72 ± 0.04	16.94 ± 0.53
Kuiseb	1.00 ± 0.04	19.29 ± 0.53
Nausgomab next to borehole (Site 2)	1.06 ± 0.06	18.64 ± 0.80
Nausgomab upriver (Site 1)	0.38 ± 0.06	15.23 ± 0.74
Kuiseb next to borehole (Site 9)	1.04 ± 0.05	18.62 ± 0.74
Kuiseb upriver (Site 4)	0.97 ± 0.05	19.96 ± 0.74

* P < 0.05, ** P < 0.01, *** P < 0.001

Carbon isotopes to determine water-use efficiency

From the sites on the Nausgomab river (1-3) going downriver, the WUE steadily decreases until Site 7. Near Gobabeb at Site 8&9 (where a borehole is present) the WUE increased again (Fig. 12). Although *F. albida* WUE was high near Gobabeb there is a significant difference between the WUE of the Kuiseb and Nausgomab rivers (Table 5) with means of -25.64 ± 0.04 ‰ and -26.65 ± 0.16 ‰ respectively. Because of this difference the Kuiseb was further analysed separately. The regression of the $\delta^{13}C$ on the position (Site 4, 6-9) on the Kuiseb river gave a correlation coefficient of $r^2 = 0.038$ with a probability of less than 0.1. The low correlation can be due to the low WUE of *F. albida* at Natab which has a very light $\delta^{13}C$ signature. Site 4,6 and 8 have higher $\delta^{13}C$ values but not as high as Gobabeb (Site 9). On the Nausgomab the trees at the two borehole sites (Site 2&3) had a higher $\delta^{13}C$ value than the non-borehole site 1 (Fig.12). But there was also no significant difference between sites near and far away from the pumping station (Table 5).

Table 5. Nested ANCOVA between the two rivers (Kuiseb and Nausgomab) and distance from the pumping station with the tree diameter as covariate using the $\delta^{13}C$ values of *F.albida*

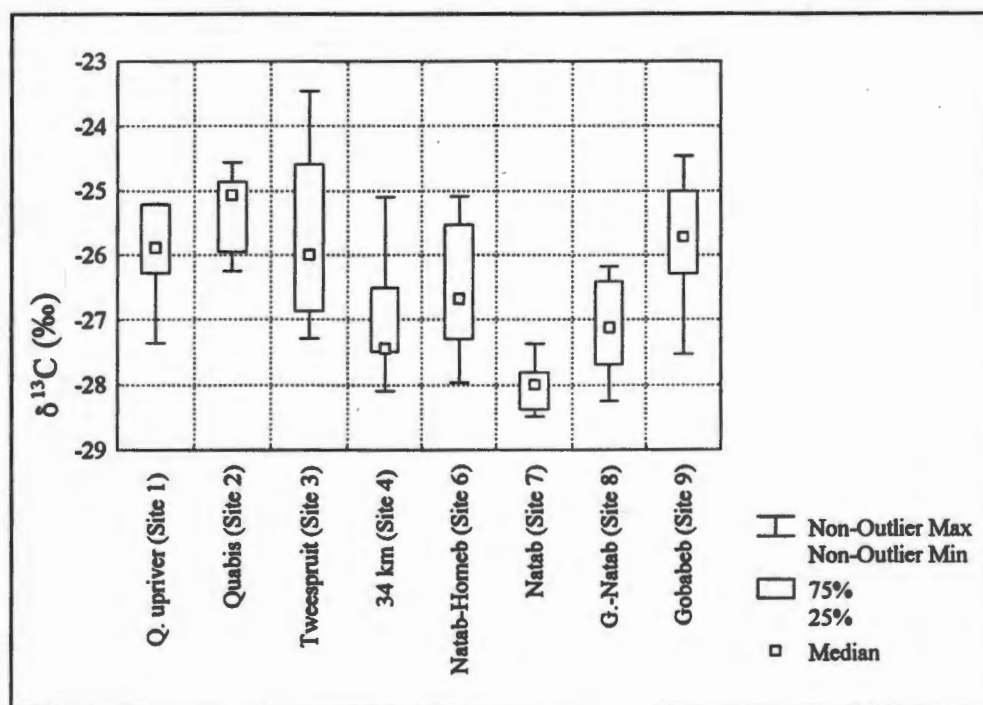|	d.f.	MS	F-RATIO
RIVER	1	16.43	15.81 ***
PUMPING	1	0.73	0.71
TREE DIAMETER	1	3.22	3.09
ERROR	71	1.04	

*P<0.05, **P<0.01, ***P<0.001

Fig. 12. $\delta^{13}C$ isotope data showing the different water-use efficiencies of *F. albida* from sites near the source of the river going towards the sea (Q=Quabis, G=Gobabeb).

There was a weak but significant negative correlation between $\delta^{13}C$ and tree diameter ($r^2 = 0.14$, P<0.001, Fig. 15). That is, the larger the tree, the less WUE it is. Testing for significance between small (stem diameter <30cm) and big (stem diameter > 30cm) *F. albida* gave a significant result with p<0.05. The big trees had a 0.7 ‰ lower mean than the small *F. albida*. This is another indication that the bigger trees are less WUE than the smaller ones. There was no significant correlation between $\delta^{13}C$ and water potentials which might have been expected if the water potentials reflected a major stress period of the plants.
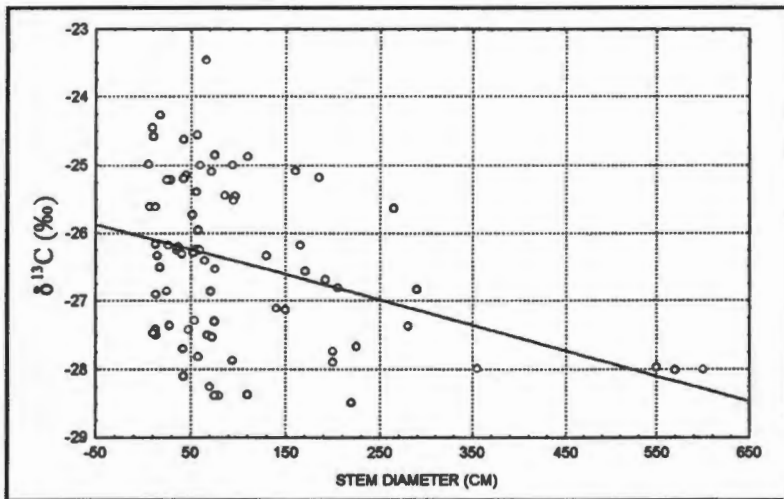
Fig. 15. Regression of $\delta^{13}C$ isotope data and tree diameter of *F.albida* with correlation coefficient 0.14 (p = 0.001)

DISCUSSION

F. albida in Namibia did not display a negative exponential size distribution as related acacia species in undisturbed areas (Walker et. al., 1986). It shows a lack of recruitment in the first size classes and many old trees at Homeb and very few old trees at Gobabeb (Fig. 4-6). The expected size structure for trees like *F. albida* is a negative exponential distribution with the number of trees declining with increasing age and size. The size class distribution of *F. albida* between 1978 and 1981 undertaken by Theron et al. (1985) was a negative exponential, despite the lack of seedlings in the Lower Kuiseb. In 1996 the recruitment problem all along the Kuiseb river appears to be more pronounced. One of the reasons for the lack of *F. albida* recruitment could be the decreased number of big flood events on the Kuiseb. The last cohort establishment of *F. albida* occurred in 1972 after the last big flood event (Robinson, 1979). At Homeb (Site 5) which has a noticeably low number of trees in the first 5 size classes, goats may also play a part in survival and may suppress growth of the seedlings. Homeb has one of the largest populations of goats along the Kuiseb river (Dausab, 1994) which trample and eat the new *F. albida* seedlings. The lack of large trees at Gobabeb in comparison with the other sites might be connected to the Desert Research Station which was established in 1959 and has a larger human population than other settlements along the river. But conservation and

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protection was in force by that time (Schoeman, 1996) and removal of trees should not have taken place. Because the size class distributions at the sites are not significantly different it would appear that the major changes *F. albida* experienced were similar along the Kuiseb river. Years with no flooding such as between 1979 and 1983, increased the mortality rate of the *F. albida* populations. Trees around Homeb were observed to die in these years (Ward and Breen, 1983). During those years an estimated 40% decline in the growth and vitality of the riverine vegetation around Gobabeb was observed (Ward, 1983 cited by Ward and Breen, 1983). It is thus possible that all population changes of *F. albida* in the area are the result of droughts and lack of flood events rather than the secondary factor of water extraction.

Since at 34km upriver, Homeb and Gobabeb on the floodplain (Site 4,5&9) the *F. albida* have significantly different amounts of dead material in their canopy it could be hypothesised that the cause of mortality must be local (Table 2, Fig 7-8). Between 1978 and 1981 a striking increase in the dead material in the canopy of *F. albida* occurred and this pattern was attributed to drought (Theron et al. 1985). The data collected in this project cannot be solely explained by drought and decreasing flood regimes but must involve local water extraction. Drought and flood regimes should affect all sites along the Kuiseb river in the same way. At the 34 km upriver site, the trees experienced stress but not as much as at Gobabeb and Homeb where pumping takes place. At Gobabeb water extraction must be the cause of the trees dying on the flood plains because there is no pumping at the 34 km upriver site. Pumping of groundwater is therefore affecting the *mortality* of *F. albida* while flood regimes and rainfall influence the *size structure* of the population. Although the pumping of water on the Kuiseb does not directly influence the recruitment of *F. albida* it is sufficient to significantly increase the mortality.

It seems that the smaller *F. albida* are the ones which are threatened most by the decrease in the water table and flood regime. The smaller *F. albida* (stem diameter < 30 cm) are less capable of handling water stress than large trees (stem diameter >30 cm). There are more dead or dying small trees along the Kuiseb river than there are old trees. Small trees have higher WUE, which indicates that their water source is not as stable as the one for the older trees. These findings are opposite to the hypothesis of Ward and Breen (1983) who proposed that the roots of smaller trees will grow along with a falling water table and therefore would

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be less water stressed. It seems more likely that the younger trees never reach the deeper ground water. The Kuiseb river aquifer is only recharged when the river flows for several days (Bate and Walker, 1993). When there are years of no recharge there is continuous extraction of water by pumping, the trees have to utilize deeper resources which are probably unavailable to the smaller trees. The decreasing flood regime and the pumping of water therefore threatens the survival of small *F. albida*. The recruitment problem of *F. albida* (Fig.4-6) will get more acute over the years if pumping is increased and floods decrease because of the construction of dams upstream.

F. albida is a tree which is dependent on a stable water source, even though it grows in the desert. This is reflected in its water potentials and $\delta^{13}C$ measurements. Many desert species exhibit a highly stable osmotic potential which results in a relative constant hydrature of protoplasm (Walter and Stadelmann, 1974). This can be achieved by faster closure of stomata to reduce water loss under drought conditions or a deep and efficient root system, which compensates by increasing water uptake for the higher transpiration losses. *F. albida* has a deep root system (Wood, 1989) and a high transpiration rate (Bate and Walker, 1993). The water potentials of *F. albida* reflect its high water requirements with a range of -0.5 to -2.2 MPa. Other deciduous trees and shrubs in the Sonoran desert displayed a range from -0.6 to -1.7 MPa while perennial shrubs which are slightly xeromorphic had a range from -2.0 to -5.7 MPa (Walter and Stadelmann, 1974).

Comparing the measurements of this project to an earlier study on *F. albida* undertaken by Ward and Breen (1983) in 1976 in the Kuiseb river gave slightly different results. This study was done at the end of April about a month after the Kuiseb river flowed for four days. Even though water conditions should have been beneficial the water potential values were in the range or below those of Ward and Breen (1983) measured in winter. The water conditions during 1976 were very favourable because the Kuiseb flooded for 61 days which increased the water table and made water easily accessible for the trees. The Kuiseb has not experienced a big flood since 1976 (Fig.2). This might explain the higher water stress for *F. albida* measured during this 1996 study when compared to earlier ones of Ward and Breen (1983).

The low WUE of *F. albida* also seems to suggest that it needs unusually high soil moisture for establishment and is expected to have high mortality under extended periods of low soil moisture availability (Ehleringer and Cooper, 1988). *F. albida* is inherently an inefficient water user because it relies on groundwater sources. The low $\delta^{13}C$ values of *F. albida* on the Kuiseb are similar to the values of trees along washes in Arizona (Ehleringer and Cooper, 1988) while the $\delta^{13}C$ values of the Nausgomab river are similar to the transition zone trees in Arizona which have less water available. The lower the $\delta^{13}C$ the less WUE the tree is and the more easily should the water be available. The *F. albida* along the Nausgomab river in the eastern Namib have a significantly higher WUE (lower $\delta^{13}C$) than the trees along the Kuiseb river in the central Namib (Table 5). The groundwater at the Nausgomab river may therefore be accessed with more difficulty by *F. albida* than in the Kuiseb river. The Kuiseb flows in large quantities in the sand aquifer of the river bed (Bate and Walker, 1993) while in the Nausgomab river no large aquifer is present. Bate and Walker (1993) estimated the Kuiseb river aquifer to be 307m wide and about 10m deep. On the Nausgomab, depth of boreholes are up to 101m deep while on the Kuiseb depths only go to 35m (Table 1). This is a good indication of how far the water is below ground. The difference in WUE of *F. albida* of the two river systems could therefore be due to the availability of ground water. Wood (1989) suggested that the tap root of *F. albida* could grow 40m deep. Trees on the Nausgomab river would therefore still encounter water problems. With the 10m deep aquifer at the Kuiseb river, water should be more easily accessible there than on the Nausgomab river.

Stewart et al. (1995) found that WUE also correlates with rainfall in the range of 350-1700 mm. The higher the rainfall the lower the $\delta^{13}C$ value. This rainfall range is far above the average rainfall of the Kuiseb and the Nausgomab river where both receive less than 200mm a year. On the Kuiseb river, Gobabeb receives a mean annual rainfall of 18.3mm and other raingauges in the vicinity of the study area have an average of about 20 mm year^{-1}. Annual fog moisture in the lower Kuiseb varies from 11.0-37.8 mm year^{-1} and may contribute a significant amount to the precipitation (Robinson and Seely, 1980; Pietruszka and Seely, 1985). On the Nausgomab river which is further east (Fig. 1), less fog occurs and mean rainfall ranges from 189 mm year^{-1} at Quabis to 121.4 mm year^{-1} at Tweespruit. The rainfall decreases with decreasing $\delta^{13}C$ in the Namib Desert (Fig.12) which is opposite to the correlation of Stewart et al. (1995). The $\delta^{13}C$ value should therefore not have shifted in response to rainfall

differences between the Kuiseb and Nausgomab river. This indicates that in arid regions the $\delta^{13}C$ value between ecosystems is independent of rainfall and is probably related to soil moisture availability.

The WUE of *F. albida* decreases from the Khomas Hochland towards the sea as water gets more readily available (Fig.12&1). The groundwater which is stored within alluvial deposits at the lower reaches of the Kuiseb provide *F. albida* trees with a stable water source. After the steady decrease of WUE going downriver it is surprising that the WUE near Gobabeb (Site 8&9) is reversing the trend by going up again (Fig. 12). The cause for this decrease in WUE of *F. albida* is probably due to the water extraction at Gobabeb for the research station and the Topnaar village. Although there is a pumping station at Natab (Site 7) the water table is near the surface (Table 1) and the WUE of the *F. albida* is very low. The water extraction at Natab therefore does not affect the water availability for *F. albida*. Near Gobabeb *F. albida* are more water stressed than on any other site of the Kuiseb river due to pumping of the groundwater. On the Nausgomab river the higher water extraction (Table 1) for the farmhouses (Site 2&3) could also be the cause of the higher WUE than at the upriver site (1) (Fig. 12). Further downstream on the Kuiseb river near Swartbank and Rooibank (Fig. 1) where the pumping for the coastal towns take place an even higher WUE of *F. albida* would be expected. If more data from further down the river is collected a significant correlation between position on the Kuiseb and $\delta^{13}C$ might be found. This would indicate that water extraction by pumping is reflected in the WUE of *F. albida* on the Kuiseb river as measured by the $\delta^{13}C$ technique.

The results of the water potential measurements differed from those of the stable carbon isotopes. From comparison of the $\delta^{13}C$ and water potential results it appears that the carbon isotope values reflect a long-term integrated water stress while the water potentials indicate point in time stress which in this study relates to the availability of the water from the last flood event. This is evident from the low correlation between the $\delta^{13}C$ and water potentials for *F. albida* in this study. Water-use efficiency and water potential should have been negatively correlated (Ehleringer et al. 1991) with the higher WUE being most often associated with more stressed plants. The water potential at certain sites also opposed the $\delta^{13}C$ results such as the pre-dawn water potentials which indicated a problem in rehydrating

the leaves during the night at sites away from the borehole on both rivers (Site 1&4) (Fig.10). The *F. albida* at the two borehole sites (Site 2&9) therefore seemed to have been less water stressed than the trees further away from the borehole. But over the long term, lower WUE of the trees at the boreholes suggest that they have more difficulties in accessing water than the trees further away from a borehole (Fig.12). Water in the soil must have still been available at the borehole sites from the last flood which would have increased the water potential measurements. The saturated sandy alluvial deposits might be closer to the surface at the borehole sites than at the upriver sites. After a flood event those sands will be saturated and water will be easily available for the trees. Evaporation and pumping might decrease this water resource rapidly, causing the trees to rely on deeper resources again. The water stress of *F. albida* at the borehole sites during the dry season then is reflected by their high WUE. Water potential is an instantaneous result for water stress while carbon isotopes indicate a season-long water stress. The $\delta^{13}C$ value included the water stress of the last dry season which would be an indication of how easily the ground water was available to the trees. For investigation of plant water problems stable carbon isotopes are a better option than water potential measurements unless those are performed on a detailed seasonal basis.

From studying the different aspects of *F. albida's* water problems on the Kuiseb and Nausgomab river it may be concluded that they are probably dying from lack of water and not natural senescence. Although there is no overall significant difference between *F. albida* near and far away from the borehole the trees seem to be more stressed near a pumping station, especially at Gobabeb where the trees have a high WUE and are dying on the flood plains. Along the Kuiseb, very few trees from the small size classes were found, which is due to combination of a recruitment problem and the high mortality of smaller *F. albida*. Both are caused by the interference of humans in the water cycle of the Kuiseb river. The damming of river flow upstream has reduced the number of flooding events and thus the recharge of the Kuiseb aquifer. With this lower water table, from water extraction or lack of recharge, the smaller *F. albida* are under water stress and often die. The lack of signifcant floods on the Kuiseb since 1976 is also a problem for the establishment of *F. albida* seedlings. If pumping of the Kuiseb river continues and more dams are built upriver *F. albida* populations will decrease steadily.

ACKNOWLEDGMENT

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