

Fig. 3. Synthesis of methionine from  $N^{5}$ methyltetrahydrofolate under the influence of methionine synthase.

methylenetetrahydrofolate. The N<sup>5</sup>-methyltetrahydrofolate so formed is then transferred to homocysteine (Fig. 3). This reaction is catalysed by two different methionine synthase enzymes, one of which requires vitamin  $B_{12}$ , and the other polyglutamate forms of the methyl folate substrate. The mechanism of the  $B_{12}$ -requiring enzyme is complex and involves the intermediate formation of methylcobalamin (Fig. 3). The methyl group is then transferred from methylcobalamin to homocysteine, giving a reduced form of vitamin  $B_{12}$  and methionine. The reduced vitamin  $B_{12}$  is possibly cob(I)alamin, or cob(II) alamin in close association with a thiolate anion. The reduced vitamin  $B_{12}$  regains a methyl group from  $N^5$ -methyltetrahydrofolate and the cycle repeats. S-Adenosylmethionine, in the presence of reduced flavin and a thiol reductant, may act as a primer in the above system, forming methylcobalamin from reduced vitamin B<sub>12</sub> inactivated by oxidation.

Sulphonium compounds play a key role in the functioning of microorganisms, plants and animals. The diversity of reactions in which S-adenosylmethionine takes part makes it almost as uniquitous in metabolism as ATP.  $\Box$ 

# Drought Stress and the Demise of Acacia albida along the Lower Kuiseb River, Central Namib Desert: Preliminary Findings

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The Kuiseb river, one of the major nonperennial watercourses traversing the Namib Desert (Fig. 1), supports a welldeveloped riverine vegetation along its lower reaches and plays an important ecological role in delimiting much of the northern boundary of the main Namib Sand Sea.<sup>1-4</sup> It has been postulated that:

a) The development of the riverine plant communities along the lower Kuiseb is largely dependent upon the availability of underground water.<sup>1</sup> If this is correct, their continued existence would be adversely affected by a decrease in the underground water reserves consequent upon drought or water abstraction for industrial and domestic use.<sup>2</sup>

b) On the basis of their distribution along the riverine fringe,<sup>2,3</sup> two of the principal species, *Acacia albida* Del. and *A. erioloba* E. Meyer, differ in their use of water.<sup>1</sup>

The Kuiseb river flooded annually past the Namib Desert Research Station (now called the Namib Research Institute) at



Fig. 1. Locality of the study area along the lower Kuiseb river, Central Namib Desert.

Gobabeb between 1962/63 and 1978/79 (Table 1).<sup>2.5</sup> Since then, however, it has not flooded into the lower reaches (Table 1) and the Kuiseb water-table in the Harubes-Soutrivier sector (Fig. 1) has dropped by more than 3 m. During this dry period, a considerable number of large mature A.

Table 1. Summarized flood history of the lower Kuiseb River at Gobabeb (after Seely et al.<sup>2</sup> and Ward<sup>5</sup>).

Year	Days of flow
1962/63	68
1963/64	No record
1964/65	26
1965/66	18
1966/67	22
1967/68	11
1968/69	18
1969/70	1
1970/71	34
1971/72	43
1972/73	15
1973/74	102
1974/75	10
1975/76	61
1976/77	8
1977/78	7
1978/79	8
1979/80	No flow
1980/81	No flow
1981/82	No flow
1982/83	No flow

albida trees have collapsed and died (Fig. 2), and C. J. Ward et al.<sup>6</sup> estimated an approximately 40% decline in the growth and vitality of riverine vegetation in the Gobabeb area between May 1978 and May 1981.

These observations have led us to assess preliminary field data on daily changes in xylem pressure potential of A. albida and A. erioloba, collected near Gobabeb before

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Fig. 2. The collapse of *Acacia albida* trees in the riverine fringe woodland near Homeb, lower Kuiseb river. Taken from above the beacon DW303, looking upstream; 2 December 1982.

and after the 1975/76 Kuiseb flood,<sup>7</sup> as they are pertinent in understanding the causes of mortality of A. albida along the lower Kuiseb river.

## Study area

Two sites close to the Namib Research Institute at Gobabeb (23°32'S, 15°03'E), representing a riverine situation (site R) and a more elevated, river terrace location (site T), were selected (Fig. 3). A large, mature A. *albida* tree was selected randomly at site R as were two A. *erioloba* trees, designated  $T_a$ and  $T_b$ , at site T (Fig. 4).

Investigations were carried out on December 17-18, 1975 and January

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17 - 18, 1976, before the 61-day flood of the 1975/76 summer, and again on July 17 - 18, 1976, some three months after the surface flow had ceased. Atmospheric conditions were warmer and more humid and the evaporation greater during the summer

Fig. 3. Oblique aerial view of the study sites near Gobabeb; 8 December 1982.

(December and January) investigations than in winter (July).<sup>8</sup>

Surface flow in the Kuiseb river had not



Fig. 4. Schematic profile of the study area showing the relative positions of site T, site R and the Kuiseb river; July 1976.

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SITE R

Fig. 5. Daily variation in temperature and vapour pressure deficit during the summer and winter investigations at the riverine site (site R) and the terrace site (site T). Black horizontal bars represent hours of darkness.

occurred for approximately 280 days prior to the December readings and only 6.6 mm of rain was measured at Gobabeb during that period.<sup>8</sup> On January 12 and 13, 1976, a further 8,4 mm of rain was recorded but over those two days evaporation was 22.3 mm.<sup>9</sup> Conditions were, therefore, relatively dry when both the December and January investigations were undertaken.

Unusually heavy rains fell in the Central Namib Desert between January 20 and 24, 1976, and 51.4 mm was recorded at Gobabeb.<sup>6</sup> This rainfall exceeded both the average for January (2.2 mm) and for the year (16.8 mm).9 Good rains in the Kuiseb catchment caused the river to start flowing past the study sites at Gobabeb on 21 January 1976, and to continue for a total of 61 days. Further rain (43.6 mm) was recorded at Gobabeb between February and April, 1976.8 A total of 95 mm was, therefore, recorded between the January and July determinations of xylem pressure potential at the study sites. The prolonged river flow, as well as the unusually high rainfall, in 1976 are likely to have recharged the groundwater reserves in the Kuiseb river between the summer and winter investigations.

## Materials and methods

Xylem pressure potential ( $\psi$ ) was measured with a Scholander pressure chamber.<sup>10.11</sup> Non-flowering shoots were sampled randomly from 1.5 m above ground-level<sup>12</sup> and  $\psi$  was estimated within two minutes.<sup>10</sup> Exclusion error<sup>13</sup> was reduced to a minimum. The chamber was pressurized evenly<sup>10.14-16</sup> and the appearance of sap was observed with a × 10 hand-lens. The chamber was not calibrated and estimates are, therefore, relative indicators of water stress.<sup>12.17</sup>

Estimates were taken at two-hourly (December and January) and three-hourly (July) intervals over a full day. Temperature and atmospheric evaporative demand (AED) were determined immediately prior to each estimation of xylem pressure potential.

#### Results

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Measurements at site R were started in the late afternoon. Temperature and vapour pressure deficit changes are recorded in Fig. 5 and  $\psi$  values are shown in Fig. 6. Temperature fluctuations were the major cause of variations in AED. The vapour pressure deficit (VPD) dropped overnight from 15.1 mb to 0.7 mb in summer and from 20.2 mb to 1.0 mb in winter, respectively, and increased again after sunrise in both instances (Fig. 5). Plant water stress reflected the changes in AED.

In summer,  $\psi$  at site R gradually increased from a minimum value of -2175 kPa through the late afternoon and night (100 kPa h<sup>-1</sup>) to a maximum of approximately -1100 kPa, with a rapid decrease (160 kPa



Fig. 6. Variations in xylem pressure potential ( $\psi$ ) recorded in Acacia albida at site R. Black horizontal bars represent hours of darkness. Vertical bars represent 95% confidence limits. —, January 1976 values; - -, July 1976 values.



Fig. 7. Variations in xylem pressure potential ( $\psi$ ) recorded for Acacia erioloba, T<sub>a</sub>, at site T. Vertical bars represent 95% confidence limits. —, December 1975 values; ---, July 1976 values.

h<sup>-1</sup>) after sunrise (Fig. 6). Despite a decrease in VPD early in the evening,  $\psi_{base}$  was not attained until shortly after midnight (-1100 kPa) and then was maintained for only about four hours. The long period taken to re-establish equilibrium ( $\psi_{base}$ ) is indicative of unfavourable soil moisture conditions.<sup>12.18</sup>

In winter, maximum water deficit ( $\psi_{min}$ ) was - 1000 kPa compared with - 2575 kPa in summer, which corresponded to a lower VPD in July. In addition,  $\psi_{base}$  appeared to be both less negative and more quickly reestablished in July (-550 kPa) than in January (-1100 kPa), suggesting more favourable soil moisture conditions at site R in winter.

Measurements at site Twere started in the early morning. Changes in temperature and vapour pressure deficit are recorded in Fig. 5 and measurements of  $\psi$  are shown in Figs 7 (T<sub>a</sub>) and 8 (T<sub>b</sub>), respectively. In summer, VPD increased from 0.8 mb in the early morning to 13.3 mb in the mid-afternoon. The corresponding values in winter were 0.6 mb and 17.6 mb, respectively. Plant water stress reflects AED, increasing to  $\psi_{min}$  during the day and becoming less negative as it approaches  $\psi_{\text{base}}$  at night.<sup>12</sup>

At site T, both A. erioloba trees (Figs 7 and 8) gave very low  $\psi$  values during the day in summer;  $\psi_{min}$  at T<sub>a</sub> was -3300 kPa and -4120 kPa at T<sub>b</sub>. In winter, however,  $\psi_{min}$ recorded for both trees (T<sub>a</sub> = -2540 kPa; T<sub>b</sub> = -2870 kPa) was less than in summer, although the VPD at site T was greater in July than in summer (Fig. 5). In addition,  $\psi_{base}$  was more negative for both T<sub>a</sub> and T<sub>b</sub> during the summer, indicating less favourable soil moisture conditions<sup>12.16</sup> then than in winter.

#### Discussion

Maximum plant water deficit, i.e.  $\psi_{min}$ , was recorded in summer for both *A. albida* at site R (-2575 kPa) and *A. erioloba* at site T (T<sub>a</sub> = -3300 kPa; T<sub>b</sub> = -4120 kPa). The estimates for both species fall within the range of  $\psi_{min}$  values recorded for desert plants in North America (-1800 to -4500 kPa).<sup>19</sup> However, these values are not unusually low for desert plants, as minimum values of -8800 kPa to -16 300 kPa have been reported for some woody species in the





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In this study, measurements were taken on different days at each site in summer. Therefore, between-site discrepancies may reflect day-to-day variation and are not necessarily consistent differences. However, consistently less negative  $\psi$  values were measured for all trees at sites R and T in July than in the summer. It is known that 'drought-avoiding' species may control xylem pressure by shedding leaves and thereby reducing transpiration. Although A. albida is generally deciduous, and A. erioloba may be partly deciduous,20 the study trees had not lost their leaves during the July investigation, so this does not account for the greater  $\psi$  values noted in winter. The retention of leaves by both species during the 1976 winter provides circumstantial evidence that the trees were not experiencing undue water stress at that time. Although the lower temperatures recorded in July than in summer may have contributed to the greater  $\psi$  values measured in winter, other factors appear to operate, for at site T VPD was greater in July than in December (Fig. 5).

Of particular significance are the consistently less negative  $\psi_{base}$  values recorded for the three trees in winter than in summer.  $\psi_{base}$  values are considered to be indicators of soil moisture conditions,<sup>10.18</sup> in which case the values noted in this study imply that soil moisture conditions were more favourable in July than during either the December or January investigations.

It is probable that the prolonged Kuiseb river flood of 1976, together with the unusually heavy rains that summer, had recharged the groundwater reserves in the river bed, at least in the vicinity of Gobabeb. It is also likely that those favourable soil moisture conditions persisted several months after the cessation, in April, of surface flow in the Kuiseb past the study site.

The Kuiseb river had flooded annually into its lower reaches, past Gobabeb, for at least 11 years prior to the 1975/76 investigations (Table 1). In contrast, there has been no surface flow at Gobabeb in the last four years (1979/80 – 1982/83) and the watertable has dropped markedly over this time. The demise of mature *A. albida* trees in the Harubes-Soutrivier sector of the lower Kuiseb can therefore probably be attributed to plant water stress induced by the lower water-table.

Significantly, localised stands of juvenile A. albida trees, mainly established after the prolonged flood of 1974 and the good rains of 1976, have continued to grow and appear to be flourishing. These stands are particularly noticeable in the Damaron-nowati, Obartaem, Gobabeb (Figs 3 and 4) and Soutrivier areas. We suggest that the roots of these quick-growing juvenile A. albida trees are able to follow the dropping watertable, whereas those of the mature trees are not because of a relatively shallow rooting system established when the water-table was relatively high.

The demise of large A. albida trees has not yet been followed by changes in status of A. erioloba along the lower Kuiseb river. This is possibly because A. albida occurs in woodland, wooded grassland and riverine fringe forest habitats, whereas A. erioloba is 'one of the major tree species of the desert regions'<sup>20</sup> (p. 234) and is thus expected to be tolerant of drought.

The preliminary results of this study indicate that a lowering of the Kuiseb watertable can be expected to affect adversely the riparian A. albida which are a vital component of the lower Kuiseb ecosystem, and substantiate the opinion of Seely et al.<sup>2</sup> that a decrease in the subterranean water reserves of the lower Kuiseb would probably be detrimental to the woody riparian vegetation.

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