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Adaptation of *Colophospermum mopane* to extra-seasonal drought conditions: site-vegetation relations in dry-deciduous forests of Zambezi region (Namibia)

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Abstract

Background: The drought-tolerant tree species *Colophospermum mopane* is focussed at for an assessment of the impact of water stress, as well as for the specific adaptation potential of the species. Three differing sites ('Forest', 'Shrubs' and 'Swamp') under three different seasonal situations (advanced dry season, drought and early rain season), in the mopane woodland of north-eastern Namibia were studied.

Methods: Plant water potentials were measured using a pressure chamber in the field. Pre-dawn water potentials were assessed to reflect the soil water potential of the rhizosphere. Midday water potentials were measured to assess the strongest negative water potential by the sample trees.

Results: The study reveals significant differences of the water potentials indicated by *C. mopane*. The different site-vegetation relations specify the impacts of seasonal conditions and site conditions (soil parameters and soil water availability) on the selected species.

Conclusions: The investigation reveals a specific adaptation potential of *C. mopane* in relation to different soil parameter under seasonal conditions. The impact of the different seasons on the pre-dawn plant water potential (indicating actual soil water availability) was assessed independently of other parameters. The adaptation range of *C. mopane* is obviously reflected by its ability to cope with water stress situations by midday samples. An advantage of using plant-physiological characteristics as monitoring parameters is the circumstance that these reflect the plant-internal 'digestibility' of the evaluated conditions directly on the natural stand. In this consideration, the evaluation of specific site conditions referring to the plant-effective water deficiency and the plant-internal, physiological ability of adaptation towards these, are recommended as key-parameters, for, e.g., investigations of site-species matching for afforestation or reforestation management.

Keywords: Mopane woodland, *C. mopane*, Site-species matching, Adaptation, Drought, Zambezi region

Background

In the expectation of a changing climate and potentially increased frequencies of drought situations, the evaluation of a tree species' adaptation potential towards water stress conditions is gaining a growing importance. While drought can be a normal and natural feature of the climate in most parts of the world, recurring or long-term drought can bring about desertification. Such extra-seasonal droughts

could be an effect of climate change (Stern 2007; WBGU 2007) as well as an accelerating factor adding to underlying causes of climate change (Prabhakar and Shaw 2008). Droughts may even accelerate deforestation and are pushing forest ecosystems towards a 'tipping point' where those would irreversibly start to die. This concerns not only dry zones, but humid areas as well. Scientists at the Brazilian National Institute of Amazonian Research, for example, argue the 2005's drought being the 'worst drought of the century' in the Amazon rainforest and leading the rainforest to the brink of being turned into savanna or desert,

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with catastrophic consequences for the world's climate (Nobre et al. 1991; Nepstad et al. 2006; Phillips et al. 2008). In this light, the identification and evaluation of more drought tolerant tree species for reforestation schemes will be of fundamental importance. This is especially important for southern Africa, where an on-going decline of tropical dry forest is attributed to population pressure and climate change related droughts (De Cauwer et al. 2016).

Often enough, it is especially the lack of knowledge on site-vegetation matching and on management of water deficiency situations that leads to the failure of reforestation programmes (Gebrehiwot et al. 2005). Especially the lack of knowledge on the biology and ecology of indigenous species and their adaptation to environmental stress limits their use in reforestation programmes. Soil water availability is one of the major limiting factors to survival, growth, species composition and distribution of savanna tree and shrub species (Mitlöhner 1998; Serrano et al. 1998; Reynolds et al. 2004; Otieno et al. 2005; Makhado et al. 2014). Hence, understanding water uptake patterns, the physiological response of the species to water stress and their tolerance to cope under severe stress are needed to explain differences among species in survival and distribution. It also allows determining a relative suitability of species for reforestation, if not restoration of degraded lands. Previous work on plant water relations emphasized the need to investigate native species and their responses to changes in water resource availability (e.g. Clifford et al. 1998; Mitlöhner 1998; Le Roux and Bariac, 1998; Rodriguez et al. 2000; Vertovec et al. 2001; Gebrehiwot et al. 2005).

The term 'site-vegetation relation' comprises the interaction between specific sites with specific plant species. By that, it is encompassing manifold factors and functions like soil conditions, climatic parameters, as well as genetic pre-conditions that, on the other hand, determine certain windows of plant-reaction and adaptation potential. The more constraining the site conditions for plant growth are, the higher need is of species' adaptation capacity and the fewer the number of species that are able to adapt and solely survive under these conditions. In this insight, this study focuses on the adaptation of *C. mopane* to seasonal and extra-seasonal water stress situations.

The goal of this investigation is to assess the adaptation of *C. mopane* to water deficiency. Variations within and between the sites under different seasonal conditions are to differentiate 'average' conditions from extra-seasonal (drought) situations and are recorded under different soil conditions.

Methods

Study species

C. mopane (Kirk ex Benth.) J. Léonard (Caesalpinioideae, Mopane) is a medium to large tree of between 4 and

18 m in height. It is dominant over large areas of southern tropical Africa in hot, low-lying regions. It is often present on alluvial as well as alkaline and poorly drained soils, which it tolerates better than other species (Palgrave 2002; Makhado et al. 2014). Its natural distribution ranges from southern Angola and northern Namibia, through Botswana, Zimbabwe and southern Zambia as far as southern Malawi, Mozambique and northern South Africa. It is commonly found at altitudes between 200 and 1200 m asl (Timberlake 1996). *C. mopane* often forms pure stands of two distinct types. On favourable sites, the stands are made up of tall trees ('cathedral mopane'), but when the soil conditions are less favourable, the vegetation is referred as to 'mopane shrub' (Palgrave 2002). The distribution of mopane is best associated with low to moderate rainfall, high temperature, low altitudes and a variety of soil types (Makhado et al. 2014). According to Mitlöhner (1997), *C. mopane* grows preferably on fine-grained sand and clay-loam sites developed from basalt, alluvial material and lime. The species is more competitive than almost any other species, especially when the sites are periodically water logged, and also on solonchic sites. Makhado et al. (2014) explain that *C. mopane* is adapted to survive moisture stress, low nutrient environments and even disturbances caused by fire and browsing by large herbivores through its physical, physiological and chemical responses.

The seeds germinate easily, but the seedlings grow slowly and are browsed by cattle and elephants. The heartwood is dark-reddish to almost black, very durable, hard and heavy. Due to its durability and availability within arid zones, it forms the most important source of poles, fuel wood, bark-rope etc. for subsistence use of local farmers in most northern parts of Namibia. According to Timberlake (1996), it can survive well in non-arable areas where other tree species struggle.

Nevertheless, McGregor and O'Connor (2002) also report a dieback of *C. mopane* in South Africa because its water requirements could no longer be met during drought years on 'dysfunctional' sites. Such sites are described as patches with decreasing water availability due to changes in the soil-water budget, as well as increasing sodium concentration. By contrast, McGregor and O'Connor observed no such dieback on sandy and fine-textured soils. *C. mopane* is an important species widely used for afforestation programmes on degraded lands all over southern Africa and arid areas of India (Timberlake 1996; Singh et al. 1999; Mashabane et al., 2001; Singh 2003).

Study site

Salambala, an area located in the eastern part of the Zambezi Region in north-eastern Namibia, was identified

as study area with *C. mopane* as dominant species of the dry-deciduous forest vegetation. This part of Zambezi Region receives 650 to 700 mm of annual rainfall; the potential evaporation varies between 2600 to 2400 mm per year (Mendelsohn et al. 2002). The rainy season usually starts in November and ends in April, with most intense amounts of precipitation occurring in February. The natural vegetation consists of forested savanna and woodlands. The mean temperature in the eastern Zambezi Region is recorded by Mendelsohn et al. (2002) as being about 22 °C. The maximum temperature is noted as between 34 °C and 36 °C while the minimum temperature is between 2 °C and 4 °C. According to Geldenhuis (1977), the highest temperature measured in Katima Mulilo (about 30 km north-west of Salambala) was 49.9 °C. Geldenhuis also states that frost nights can occur once a year. At an average altitude of ca. 930 m a.s.l., the eastern Zambezi Region area is generally flat as it originates from a dried-up swamp-delta of the Zambezi, Kwando, Linyanti and Chobe rivers (Mendelsohn and Roberts 1998). These rivers define the borders of eastern Zambezi Region to the east, south, west, and partly to the north (see Fig. 1). In general, the soil in the eastern Zambezi Region consists of fersiallitic soils in the north-western areas and alluvial soils in the east and south (wetlands, open grassland and swamps). A belt of solonetzic and planosolic soils is found between these

two soil types. Table 1 characterises the soil conditions of the research sites within this belt in more detail.

The Salambala location is situated in the centre of the Salambala Conservancy. This conservancy was commenced in 1995, and since fenced and protected by communal guards. An overall goal of the conservancy is the protection of the Salambala Forest as core wildlife area for nature conservation purposes. Human population (17 families living on 930 km²) was resettled during establishment (Salambala Conservancy management authorities, pers. com.). While the area is protected by the conservancy, the natural vegetation can be regarded as having no impact from people and livestock since 1995; signs of browsing, chopping or wood collection were not observed during data collection. According to local records, Salambala was neither exposed to fires nor to floods while under conservancy administration (Salambala Conservancy management authorities, pers. com.). The flora and fauna have been recorded in inventories and described by Mendelsohn and Roberts (1998). Three different sites were identified within the area described by Mendelsohn and Roberts as ‘Mopane-Aristida Woodland on Clay Loam’. The location of the sites ‘Forest’, ‘Shrubs’ and ‘Swamp’ are illustrated in Fig. 2. The names of the sites were chosen

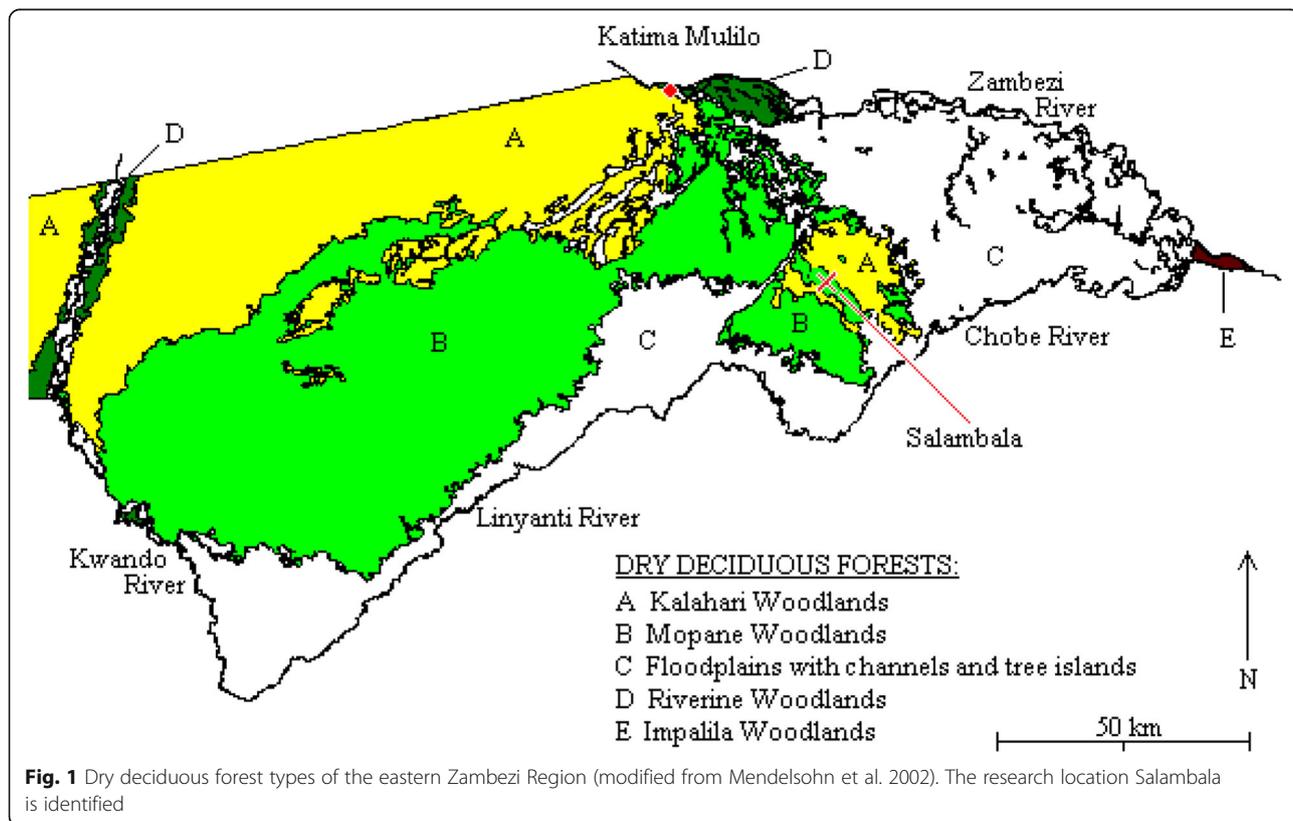


Table 1 Soil status of the research sites at Salambala. The samples were taken in the centre of the respective sites. SAR represents the sodium absorption ratio. EC stands for electric conductivity, a proxy for salinity (Soil analysis by the Soil Laboratory, Ministry of Agriculture, Water and Rural Development, Windhoek). Since the site 'Shrubs' was showing two distinct layers, both layers were sampled

Sample site (depth)	Chemical characterisation			Texture (Vol%)		
	pH _{h2o}	EC _{h2o} (mS·cm ⁻¹)	SAR (meq·L ⁻¹)	Sand (> 0.063 mm)	Silt (0.063–0.002 mm)	Clay (< 0.002 mm)
'Forest' (40–80 cm)	5.75	2.89	6.09	51.6	29.4	19.0
'Shrubs' (0–60 cm)	8.73	1.44	28.36	60.3	13.6	26.1
'Shrubs' (60–150 cm)	7.63	0.12	0.21	96.9	1.4	1.7
'Swamp' (40–80 cm)	7.74	0.61	1.76	53.6	17.2	29.2

according to visual observations, compare Table 2. Table 2 describes the respective stand structures.

Data collection and analysis

For each site, an area of 2500 m² (50 m × 50 m) was demarcated. Within those areas, all trees with a minimum diameter at breast height (dbh) of 10 cm were recorded by their dimensions (dbh and height, h), positions and crown parameters. Six to nine trees on each site were randomly selected and assessed for their plant water potentials at pre-dawn and midday. Every leaf sample taken was repeated twice. The trees within the research sites were marked permanently so that the same individuals could be re-measured. Water potential of some sample trees was not recorded in all seasons due to their lack of leaves in the on-going dry season. The assessments were carried out under the following different seasonal conditions:

August 2001:	Advanced dry season: trees are starting to drop their leaves. The last rainy season (Nov. 2000 to April 2001) had provided a very good precipitation rate of 835 mm (mean annual precipitation: 650 to 700 mm).
June 2002:	Drought: due to a very poor rainy season (2001/2002: 276 mm) a meaningful water-deficiency existed; many trees were already dropping their leaves.
November 2002:	Early rainy season 2002/2003: 119 mm had been recorded since October 2002.

The measurements of plant water potentials have gained wide-spread acceptance as useful tools for plant-water status assessments (i.e. Schmidt-Vogt 1980; Kramer and Boyer 1995; Gebrekirstos et al. 2006) and are used here to reflect site-vegetation relations. Plant water potential was measured by leaf samples using a pressure chamber (Scholander et al. 1965), which is a method widely used (Sellin 1996; Mitlöhner 1998; Rodriguez et al. 2003; Krug 2004; Gebrehiwot et al. 2005; Gebrekirstos et al. 2006). Extensive reviews on the pressure chamber measurements are available (e.g. Tyree

and Hammel 1972; Ritchie and Hinckley 1975; Boyer 1995; Richter 1997). In line with Horton et al. (2001a, 2001b), Mitlöhner (1995, 1998), Teskey and Hinckley (1986), and Hennessey and Dougherty (1984), the pre-dawn water potential is understood to reflect the soil water potential of the rhizosphere, which affects the assessed trees. The water potential assessed at midday describes the strongest negative water potential applied by the sample species to access soil water at the given measuring time. It is anticipated that leaf water potential is a species-specific parameter independent of age or size of sample trees as long as the development status and position of sample leaves are comparable: The leaf samples were taken from the same part of a branch and the same insertion height and exposure: The height of two to three metres at the western exposure of trees was chosen and only fully developed leaves of about the same age status were selected. The pressure chamber measurements were carried out in the field, at each tree as the leaf was picked.

The analysis of recorded data was carried out using QED and SPSS: After verifying the data's normal distribution and the homogeneity of variance, the means were evaluated with a one-way ANOVA test. Additionally, the Tukey test (Tukey's Honestly Significant Difference, LSD test) was carried out to distinguish significant mean differences between sites (Fowler et al. 1998). According to these procedures, all results presented are statistically significant at $P < 0.05$.

Results

The assessed stand structure (Table 2) describes noticeable differences between the three sites. While the site 'Forest' represents a typical *C. mopane* stand with a mean diameter of 29.5 cm at breast height (compare e.g. Sebege and Arnberg 2002), the site 'Shrubs' is characterised by rather dispensed mopane shrubs (mean dbh 14.0 cm, compare Palgrave (2002)). The site 'Swamp', on the other hand, is a mixed stand of dominating *C. mopane* and *Philenoptera violacea* (Klotzsch), Schrire (Fabaceae, Rain Tree). This stand

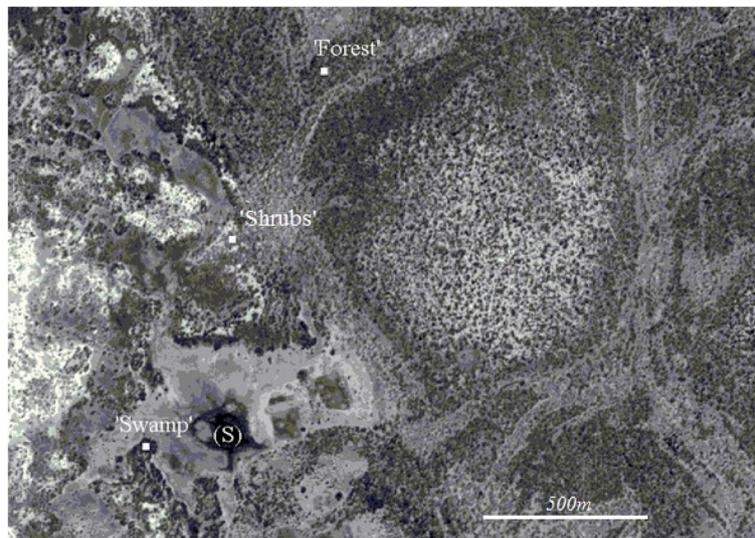


Fig. 2 Aerial photo from 1996 of the research sites at Salambala. The distance between the sites 'Forest', 'Shrubs' and 'Swamp' is 610 and 920 m, respectively; the photo is adjusted towards north. Every site measures 50 m × 50 m; (S) indicates the centre of a swamp

is benefiting by improved water availability due to an open swamp at about 30 m distance, reflected by a greater basal area than both previous stands. The stand structures are mirrored by the soil analysis of the different sites (Table 1). Especially the site 'Shrubs' is characterised by a clearly higher proportion of sand and – most notably – two considerably different soil layers within 150 cm depth.

The water potentials assessed in August 2001 reflect a situation where all three stands indicate an overall mean pre-dawn water potential with low standard deviation (SD) of $-1.60 (\pm 0.43)$ MPa and midday values of around $-4.19 (\pm 0.32)$ MPa. The major outliers are pre-dawn values of 'Shrubs' and midday values of 'Swamp', compare Table 3. In contrast to that, the results of June 2002, the drought situation, present a significantly stronger tension within the soil-plant-continuum: The mean diurnal ranges (as difference between the pre-dawn and midday water potential) in August 2001 ($2.58 (\pm 0.04)$ MPa) change to a significantly reduced diurnal mean in June 2002 of $1.15 (\pm 0.18)$ MPa. It is especially the site 'Forest' that indicates a reduced diurnal range under drought conditions of $0.54 (\pm 0.25)$ MPa. It is

remarkable that even the research site 'Swamp' indicates a less balanced situation under drought conditions (a diurnal range of $1.16 (\pm 0.57)$ MPa) than the site 'Shrubs': $1.76 (\pm 0.72)$ MPa.

To visualize and evaluate the range of re-saturation within the different sites and to assess the seasonal impact on plant water availability, the values of mid-day and predawn water potential are used as the Y- and X-axes, respectively, and a 45° bisecting line was plotted on a graph in Fig. 3. Here again, the results for August 2001, the dry season, are indicating a fairly balanced situation: All records reflect a fair distance towards the 45° bisecting line. In June 2002, on the other hand, the indications are much closer to the 45° bisecting line, by that indicating a stronger tension within the plant-water supply as to be expected. Nevertheless, especially the site 'Shrubs' indicates the most remarkable re-saturation values.

Only the water potentials recorded in November 2002 (Table 3 and Fig. 3) do not indicate meaningful differences between sites and with regard to seasonal impacts. After some 119 mm rainfall since October 2002, the diurnal

Table 2 Stand structure of the research sites at Salambala, recorded in August 2001. Only *C. mopane* was assessed for its water potential (\pm SD)

Site	Vegetation (Number of observations in brackets)	Basal area ($\text{m}^2\cdot\text{ha}^{-1}$)	Mean dbh (cm)	Mean height (in m)	Mean height (h_{10} in m)
Forest	pure <i>C. mopane</i> stand, 196 trees·ha ⁻¹ (49)	14.93	29.52 ± 11.02	9.9 ± 2.17	11.70 ± 0.42
Shrubs	pure <i>C. mopane</i> stand, 304 trees·ha ⁻¹ of poor growth (76)	6.63	14.03 ± 9.06	6.46 ± 3.25	10.73 ± 0.88
Swamp ^a	<i>C. mopane</i> stand ($17.48 \text{ m}^2\cdot\text{ha}^{-1}$, 408 trees·ha ⁻¹) with mixed <i>Philenoptera violacea</i> ($3.01 \text{ m}^2\cdot\text{ha}^{-1}$, 56 trees·ha ⁻¹) (102)	20.49	21.04 ± 11.00	8.30 ± 2.33	11.70 ± 0.61

^aA permanent waterhole nearby (30 m in north-eastern direction) creates a small swamp

Table 3 The mean plant water potential (\pm SD) of *C. mopane* recorded at Salambala in different seasons (dry season in August 2001, ‘extreme’ dry season in June 2002 and early rainy season in November 2002). The Number of observations is in brackets; all means are significant at $P < 0.05$ (Tukey LSD test)

Date, site			Plant water potentials (MPa)		
			Pre-dawn	Midday	Diurnal range
Aug 2001	Forest	(8)	-1.46 ± 0.21	-4.44 ± 0.25	2.98 ± 0.31
	Shrubs	(6)	-2.25 ± 0.17	-4.42 ± 0.31	2.17 ± 0.27
	Swamp	(6)	-1.10 ± 0.03	-3.70 ± 0.40	2.60 ± 0.38
Jun 2002	Forest	(9)	-4.28 ± 0.38	-4.82 ± 0.38	0.54 ± 0.25
	Shrubs	(8)	-3.46 ± 0.49	-5.23 ± 0.48	1.76 ± 0.72
	Swamp	(7)	-2.99 ± 0.73	-4.14 ± 0.45	1.16 ± 0.57
Nov 2002	Forest	(8)	-2.66 ± 0.25	-3.46 ± 0.33	0.80 ± 0.38
	Shrubs	(6)	-3.05 ± 0.32	-3.47 ± 0.33	0.36 ± 0.29
	Swamp	(6)	-2.63 ± 0.21	-3.15 ± 0.23	0.52 ± 0.29

ranges vary around means of $0.5 (\pm 0.04)$ MPa within the different stands.

Discussion

The different seasonal conditions were expected to have a considerable impact on the soil-water status. Following Mitlöhner (1995, 1998), the mean values of the pre-

dawn water potential are understood reflecting the soil water availability within the rhizosphere, while the mean values of the plant water potential at midday are picturing the internal availability of water in the plant in the actual, least favourable situation. In this insight, the pre-dawn water potentials indicate the seasonal differences of the soil water status, and the midday water potential

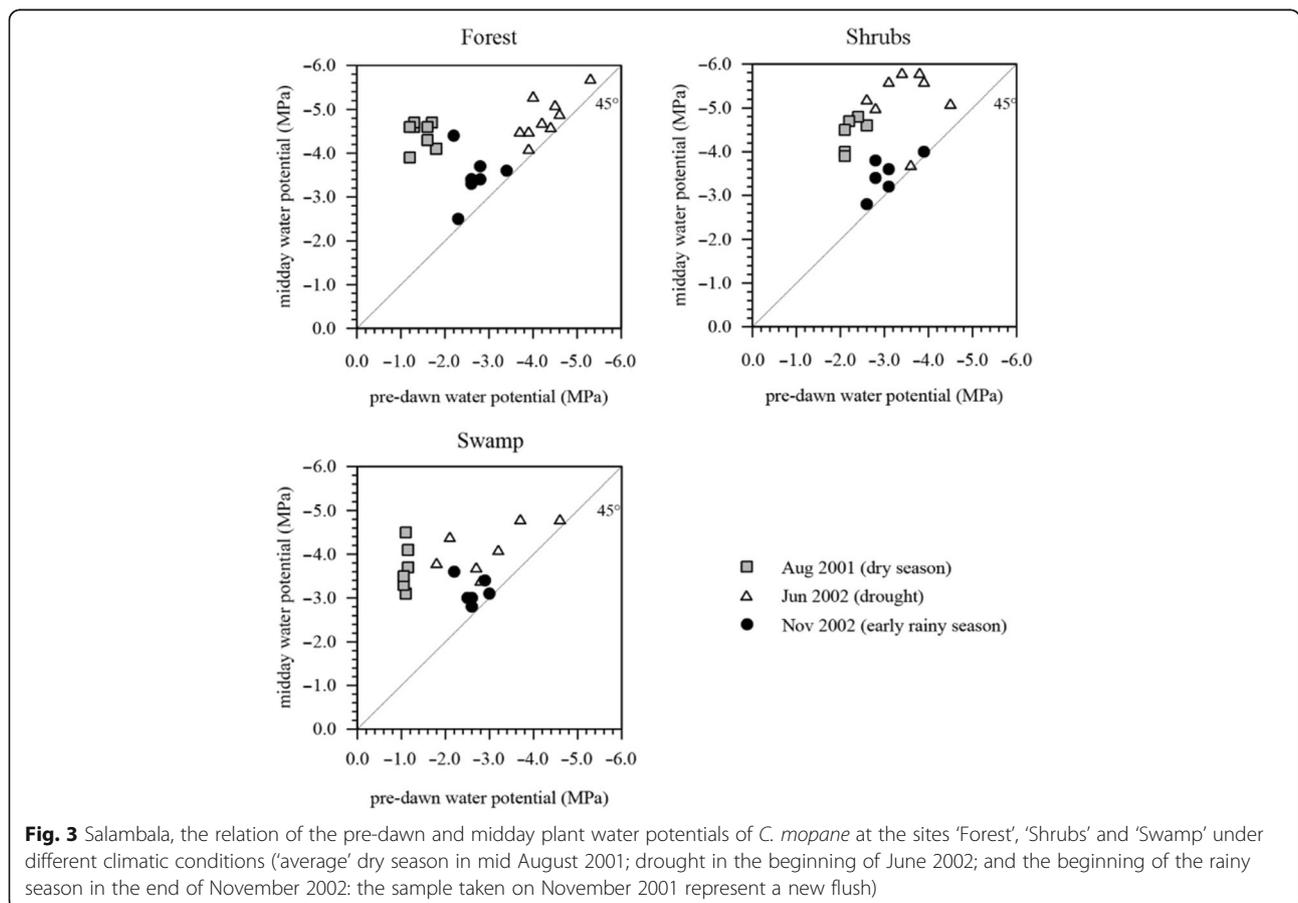


Fig. 3 Salambala, the relation of the pre-dawn and midday plant water potentials of *C. mopane* at the sites ‘Forest’, ‘Shrubs’ and ‘Swamp’ under different climatic conditions (‘average’ dry season in mid August 2001; drought in the beginning of June 2002; and the beginning of the rainy season in the end of November 2002: the sample taken on November 2001 represent a new flush)

indicates the species' specific ability of adaptation toward the current situation.

At the site 'Forest', for example, the pre-dawn water potentials indicate a notable decrease in soil water availability between August 2001 and June 2002 (pre-dawn $-1.46 (\pm 0.21)$ MPa and $-4.28 (\pm 0.38)$ MPa, respectively, compare Table 3, Fig. 3). This can be explained by a severe drought in June 2002, since the rainy season normally lasts until April but ended before February in 2002. The low rainfall of that season is expected to reduce the water availability for vegetation. However, the tree's adaptation at midday does not indicate such a noteworthy change: While the midday water potential reaches up to $-4.44 (\pm 0.25)$ MPa in August 2001, in June 2002 it shows only slightly stronger values of $-4.82 (\pm 0.38)$ MPa. This implies that the water availability in August 2001 is bearable for *C. mopane*, while it comes closer to the species-specific limit in June 2002. The strongest plant-internal water potential measured on *C. mopane* at 'Forest' was at about -5.80 MPa on a tree that had already shed most of its leaves. In comparison, Mitlöhner (1997) recorded plant water potentials on *C. mopane* at the arid Etosha Pan in northern Namibia, in the dry season of September 1991. The figures recorded were: at pre-dawn $-2.0 (\pm 0.5)$ MPa ($N = 15$), and at midday $-3.1 (\pm 0.7)$ MPa ($N = 15$). The strongest value Mitlöhner recorded was -3.8 MPa. This emphasises the stressful conditions described here for Salambala in June 2002. Maréchaux et al. (2015) describe the "leaf water potential at wilting or turgor loss point" as the most appropriate determinant for the tolerance of drought stress and refer to maximum values of 1.4 – 3.2 MPa in an Amazonian forest. Although stronger values are to be expected in a dry-deciduous forest in southern Africa, it is remarkable that leaf water potentials close to -5 MPa are recorded. Since sample trees within the site 'Forest' already dropped many of their leaves, an approximation to the wilting point can be assumed. Breshears et al. (2008) describe observations of tree die-off in response to global change-type drought by plant water potential measurements: A die-off was related to leaf water potentials remaining "substantially below their zero carbon assimilation point for at least 10 months prior to dying" (compare Sevanto et al. 2014). No such long drought was observed at Salambala, but a very small diurnal range (like at 'Forest' in June 2002) suggests a (temporary) approximation towards assimilation constrictions.

The values of November 2002 reflect a very different situation since the new vegetation period started with the first rains in late October. Nevertheless, the pre-dawn water potential was still stronger for all sites at the beginning of the rainy season in 2002 than it was in the dry season in August 2001. This indicates that the low level of rain received in this season (119 mm since October) was not yet

having a notable relief effect on the soil water availability. It was still being affected by the poor rainy season of 2001/2002 and indicates a pre-dawn water potential at 'Forest' of $-2.66 (\pm 0.25)$ MPa. The midday water potential ('Forest') indicates a value of $-3.46 (\pm 0.33)$ MPa, thus showing improved soil water availability when compared to the previous 5 months. These findings support Rodriguez et al. (2000), who researched the relationship of the plant water potential to the soil water availability by measuring diurnal and seasonal plant water potentials in Mexico. Gonzales' findings on a "strongly associated" relation within dry periods are consistent with the results from Salambala.

The investigations at the sites 'Shrubs' and 'Swamp' show the same effects of the poor rainy season (June 2002) and a relaxation with the beginning of the new rainy season of November 2002. For the site 'Shrubs', on the one hand, it is remarkable that the pre-dawn water potential is clearly stronger in August 2001 than at 'Forest' at the same time (Fig. 3). On the other hand, the value at 'Shrubs' in June 2002 is lower than the value recorded at 'Forest' (pre-dawn water potential: $-3.46 (\pm 0.49)$ MPa in June 2002, compared to $-4.28 (\pm 0.36)$ MPa at 'Forest'). 'Shrubs' clearly experiences higher water stress under 'average' conditions, even though it seems to be better balanced under drought conditions. The sample trees did not build up such an extreme water potential under the stressful conditions of June 2002 as the site 'Forest'.

The higher stress under 'average' conditions is reflected in the poor growth of the trees on that site (Table 2). The soil characteristics for 'Shrubs' indicate a more problematic site than 'Forest': A top layer of ca. 60 cm depth shows a high proportion of clay and silt (Table 1). The high sodium adsorption ratio (SAR) of this layer, in particular, highlights a tendency towards hyromorphic swelling and shrinking processes. According to Rhoades (1990), these processes must be considered in soil layers which exceed a SAR value of $15 \text{ meq}\cdot\text{L}^{-1}$. The SAR of this layer at 'Shrubs' shows almost double this value: $28.4 \text{ meq}\cdot\text{L}^{-1}$. In contrast, the underground layer consists mainly of sand with a very poor sodium-adsorption ratio. According to Ganssen (1968), such a solonetzic soil type can be formed by changing humid and dry conditions and the leaching of the underground layers. While the top layer forms an almost impenetrable infiltration barrier, it tends to be water logged in the rainy season and forms deep soil surface cracks in the dry season. Mensching (1990) points out however, that such an impenetrable layer can also have positive effects. As an evaporation barrier, it supports the storage of soil humidity in the deeper layers, which is thus saved for plants able to penetrate through the hard top layer. It may be assumed that *C. mopane* takes advantage of such a condition. This could explain the more moderate increase of the pre-dawn

water potential at the site 'Shrubs' under the drought conditions in June 2002 compared to the site 'Forest'. The different soil type in the upper levels has presumably been penetrated to reach more favourable conditions of the deeper, sandy soil layer.

The site 'Swamp' is characterised by a more relaxed pre-dawn water potential already in August 2001 compared to the other sites. This is a noticeable indication of the impact by the nearby Swamp. Here the consequence of an enhanced water stress resulting from the poor rainy season obviously has very little effect. These results are supported by the figures in Table 2: The site 'Swamp' shows the biggest basal area per ha of all three sites, although while the mean diameter per ha is smaller than at 'Forest'. At 'Swamp', the trees are of more or less the same diameter-group. These conclusions are supported by Mitlöhner (1998) who related stand structure parameter, i.e. diameter distribution as a proxy for dominance, to plant water potential. Comparing the stand structure described by plant morphological parameters in Table 2 with the plant physiological records in Table 3, it becomes obvious that these records - and especially the diurnal ranges - are reflected by the structure of the stands.

To judge the differences of the three sites within the different seasons in more detail, Fig. 3 illustrates the plant water potentials in relation to the midday values: The impact of the 'average dry season' (August 2001), the 'drought' (June 2002) and the 'early rainy season' (November 2002) on the site 'Forest' can be distinguished clearly by a remarkable grouping of the recorded values. The previously described findings are supported here again. At 'Forest', the trees' midday water potential is already quite strong in August 2001 (-3.90 to -4.70 MPa), while the pre-dawn water potential is still fairly low (below -2.00 MPa). This demonstrates that *C. mopane* is well suited to the site and its present conditions. It can still apply a significantly higher negative water potential than currently required. In the re-saturation phase at night, the trees build up only half the negative water potential than at midday.

This situation changes in June 2002: The markers situated closer to the diagonal line indicate a more stressful situation and that the ability of *C. mopane* to obtain soil water is approaching the species-internal limit. The pre-dawn value (the status of re-saturation over night) and the midday value (the status of the actual highest water-deficiency) are closer together. Such a small difference between the soil water status and the species' least favourable situation indicate a fairly stressful condition. For November 2002, again the value group clearly indicates the more relaxed situation: The pre-dawn water potentials which are lower than in June 2002 are also reflected by the lower midday water

potential. The midday water potential being close to the diagonal line can be explained by the fact that the beginning of the rainy season lowers the midday plant water potential, but the situation is still less relaxed than in August 2001, since the pre-dawn water potential is still strong.

Comparing these findings with the illustration of the site 'Shrubs' (Fig. 3), it is clear that the plant-available water resources are accessed with a higher tension, hence a stronger potential is built up. Most of the samples indicate a pre-dawn water potential between -2.0 and -4.0 MPa, independent of the season. This again indicates a constrictive but as well balancing impact in the soil, like the evaporation barrier described by Mensching (1990). It is specifically the adaptation of the trees that reflects the different seasons: While the midday values for August 2001 range mainly between -3.80 and -4.80 MPa, in June 2002 they are indicating stronger values than -5.00 MPa (with one exception). In November 2002 the trees show lower maximum potentials than -4.00 MPa, thereby reflecting the start of the new vegetation period.

The results for the site 'Swamp' follow the previous observations. The pre-dawn water potentials indicate obvious differences according to the more or less stressful seasons. The values however, which always show a clear distance from the diagonal line, reflect much more favourable water availability than at the other sites. In August 2001 it is clear that the pre-dawn water potential remains fairly constant (1.1 ± 0.03 MPa), despite the fact that the samples apply different high values of the midday water potential. This is an indication of a soil-water supply independent of evaporation processes and atmospheric saturation deficiencies. The results for June 2002, the 'drought', still reflect an availability of soil water (no record exceeds the value of -5.0 MPa), but distinguish between sample trees with a more or less favourable water access among the group.

The results of the investigations in November 2002 reflect a different situation at all three sites. On the one hand, it can be assumed that the new rainy season causes a lower pre-dawn water potential, but on the other hand, it is doubtful that the precipitation recently received (119 mm since October 2002) is already affecting the rhizosphere. As the results from the different sites are quite similar and even (making a differentiation by site almost impossible) it must be rather assumed that these records reflect a species-specific process. Given that all sample trees are in a new growing season, it must be supposed that the new flush does not yet allow for a differentiation of sites.

Conclusion

Summarising these results, the seasonality and its impact on the different sites are clearly reflected by plant-internal water potentials of *C. mopane*. The impact of the different

seasons on the pre-dawn plant water potential (indicating the actual soil water availability) was assessed independently of other parameters. The adaptation range of *C. mopane* is obviously reflected by its ability to cope with water stress situations by midday samples. A specific trait of *C. mopane* was observed by its ability to overcome a water-logging soil layer and to penetrate into deeper soil layers. By this, the sample trees presumably gained some access to soil water which is not accessible otherwise.

The investigations indicate a range of plant-reaction and adaptation potential, which in turn could allow identifying further species potentially adapted to the specific site conditions, e.g. for reforestation plans: The methods applied enable a qualification of the investigated stand in concern of soil water availability affecting *C. mopane*. Following this, it can be recommended to evaluate, e.g., degraded sites in a same way, combined with an investigation of the species-specific adaptation potential of desired species for reforestation and thus improve site-species matching.

In this consideration, the evaluation of specific site conditions referring to the plant-effective water deficiency and the plant-internal, physiological ability of adaptation towards these, are recommended as key-parameters, for, e.g., afforestation and reforestation activities in arid lands, or as an approach for bio-monitoring of declining vegetation types in arid zones. It can be recommended to be used for site-species matching, for an identification of suitable species for a specific site under water stress conditions. The outstanding advantage of using plant-physiological characteristics as monitoring parameters is revealed as they reflect the plant-internal 'digestibility' of the evaluated conditions directly on the natural stand.

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Competing interests

The author declares that he has no competing interests.

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References

- Boyer JS (1995) Measuring the water status of plants and soils. Academic Press, Inc., San Diego
- Breshears DD, Myers OB, Meyer CW, Barnes FJ, Zou CB, Allen CD, McDowell NG, Pockman WT (2008) Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Front Ecol Environ* 7(4):185–189
- Cauwer VD, Geldenhuys CJ, Aerts R, Kabajani M, Muys B (2016) Patterns of forest composition and their long term environmental drivers in the tropical dry forest transition zone of southern Africa. *Forest Ecosyst* 3:23
- Clifford SC, Arndt SK, Corlett JE, Joshi S, Sankhala N, Popp M, Jones H (1998) The role of solute accumulation, osmotic adjustment and changes in cell wall elasticity in drought tolerance in *Zizyphus mauritiana* (Lamk.) *J Exp Bot* 49(323):967–977
- Fowler J, Cohen L, Jarvis P (1998) Practical statistics for field biology. Wiley, West Sussex
- Ganssen R (1968) Trockengebiete, Böden, Bodennutzung, Bodenkultivierung, Bodengefährdung. Mannheim, Zürich. Bibliographisches Institut Mannheim 1968 = BI-Hochschultaschenbücher Bd. 354/354a
- Gebrehiwot K, Muys B, Haile M, Mitlöhner R (2005) The use of plant water relations to characterize tree species and sites in the drylands of northern Ethiopia. *J Arid Environ* 60(4):581–592
- Gebrekirstos A, Teketay D, Fetene M, Mitlöhner R (2006) Adaptation of five co-occurring tree and shrub species to water stress and its implication in restoration of degraded lands. *For Ecol Manag* 229:259–267
- Geldenhuys CJ (1977) Bosbestuursplan Nakabunze Reservaat: Oos Zambezi. Saasfeld Bosnavorsingstasie. Report, George, South Africa
- Hennessey TC, Dougherty PM (1984) Characterisation of the internal water relations of loblolly pine seedlings in the response to nursery cultural treatments: implications for reforestation success. In: Duryea ML, Brown GN (eds) Seedling physiology and reforestation success. Springer, Dordrecht, Boston, Lancaster
- Horton JL, Kolb TE, Hart SC (2001a) Physiological response to groundwater depth varies among species and river flow regulation. *Ecol Appl* 11(4):1046–1059
- Horton JL, Kolb TE, Hart SC (2001b) Responses of riparian trees to inter annual variation in ground water depth in a semi-arid river basin. Northern Arizona University, Flagstaff, AZ 86011–5018
- Kramer PJ, Boyer JS (1995) Water relations of plants and soils. Academic Press, New York
- Krug J (2004) Site-species matching and planting techniques for arid-zone forestry in Namibia. Dissertation, Georg-August-University of Göttingen
- Le Roux X, Bariac T (1998) Seasonal variations in soil, grass and shrub water status in a west African humid savanna. *Oecologia* 113(4):456–466
- Makhado RA, Mapaure I, Potgieter MJ, Luus-Powell WJ, Saidi AT (2014) Factors influencing the adaptation and distribution of *C. mopane* in southern Africa's mopane savannas – a review. *Bothalia* 44(1):1–9
- Maréchaux I, Bartlett MK, Sack L, Baraloto C, Engel J, Joetzer E, Chave J (2015) Drought tolerance as predicted by leaf water potential at turgor loss point varies strongly across species within an Amazonian forest. *Funct Ecol* 29(10):1268–1277
- Mashabane LG, Wessels DCJ, Potgieter MJ (2001) The utilisation of *C. mopane* by the Vatsonga in the Gazankulu region (eastern Northern Province, South Africa). *S Afr J Bot* 67(2):199–205
- McGregor SG, O'Connor TG (2002) Patch dieback of *C. mopane* in a dysfunctional semi-arid African savanna. *Aust Ecol* 27(4):385–395
- Mendelsohn J, El Obeid S, Roberts C (2002) A profile of north-central Namibia. Gamsberg Macmillan, Windhoek
- Mendelsohn J, Roberts C (1998) An environmental profile and atlas of Zambezi. Gamsberg Macmillan, Windhoek
- Mensingh H (1990) Desertifikation: ein weltweites Problem der ökologischen Verwüstung in den Trockengebieten der Erde. WissBuchges, Darmstadt
- Mitlöhner R (1995) Standortcharakterisierung durch pflanzliche Saugspannung und potentiellen osmotischen Druck in Chaco Central, Paraguay. Report. Göttingen
- Mitlöhner R (1997) *C. mopane*, III-4, 10. Erg. Lfg. 12/97. In: Weisgerber H, Roloff A, Lang UM, Schuck HJ, Schütt P (eds) Encyklopädie der Holzgewächse: Handbuch und Atlas der Dendrologie. Landberg am Lech
- Mitlöhner R (1998) Pflanzeninterne Potentiale als Indikatoren für den tropischen Standort. Aachen
- Nepstad D, Moutinho P, Soares B (2006) The Amazon in a changing climate: large-scale reductions of carbon emissions from deforestation and Forest impoverishment. IPAM, WHRC, and UFMG, Belem, Para, Brazil
- Nobre CA, Sellers PJ, Shukla J (1991) Amazonian deforestation and regional climate change. *J Clim* 4(10):957–988
- Otieno DO, Schmidt MW, Adiku S, Tenhunen J (2005) Physiological and morphological responses to water stress in two acacia species from contrasting habitats. *Tree Physiol* 25(3):361–371
- Palgrave KC (2002) Trees of southern Africa. In: Struik, cape town, new edn
- Phillips O, Lewis SL, Baker TR, Chao KJ, Higuchi N (2008) The changing Amazon forest. *Philos Trans R Soc B* 363(1498):1819–1827
- Prabhakar SVRK, Shaw R (2008) Climate change adaptation implications for drought risk mitigation: a perspective for India. *Clim Chang* 88(2):113–130

- Reynolds JF, Kemp PR, Ogle K, Fernández RJ (2004) Modifying the pulse reserve paradigm for deserts of North America: precipitation pulses, soil water and plant responses. *Oecologia* 141(2):194–210
- Rhoades JD, Shouse PJ, Alves WJ, Manteghi NA, Lesch SM (1990) Determining soil salinity from soil electrical conductivity using different models and estimates. *Soil Sci Soc Am J* 54:46–54. doi:10.2136/sssaj1990.03615995005400010007x
- Richter H (1997) Water relations of plants in the field: some comments on the measurement of selected parameters. *J Exp Bot* 48(1):1–7
- Ritchie GA, Hinckley TM (1975) The pressure chamber as an instrument for ecological research. *Adv Ecol Res* 9(9):165–254
- Rodríguez HG, Cantu Silva I, Gomez Meza MV, Jordan WR (2000) Seasonal plant water relationships in *Acacia berlanieri*. *Arid Soil Res Rehabil* 14(4):343–357
- Rodríguez HG, Silval C, Meza G, Lozanoc RG (2003) Plant water relations of thornscrub shrub species, north-eastern Mexico. *J Arid Environ* 58:483–503
- Schmidt-Vogt H (1980) Characterization of plant material. In: Proc. of the IUFRO-meeting, Freiburg i.Br., Federal Republic of Germany, 23–26 June 1980
- Scholander PF, Hammelt HT, Bradstreet ED, Hemmingsen EA (1965) Sap pressure in vascular plants. *Sci* 148:339–346.
- Sebego RJG, Arnberg W (2002) Interpretation of mopane woodlands using air photos with implications on satellite image classification. *Int J Appl Earth Obs Geoinf* 4(2):119–135
- Sellin A (1996) Base water potential of *Picea abies* as characteristics of the soil water status. *Plant Soil* 184:273–280
- Serrano R, Mulet JM, Rios G, Marquez JA, de Larrinoa IF, Leube MP, Mendizabal I, Pascual-Ahuir A, Proft M, Ros R, Montesinos C (1998) A glimpse of the mechanism of ion homeostasis during salt stress. *J Exp Bot* 50:1023–1036
- Sevanto S, McDowell NG, Dickmann LT, Pangle R, Pockmann WT (2014) How do trees die? A test of the hydraulic failure and carbon starvation hypothesis. *Plant Cell Environ* 37(1):153–161
- Singh G (2003) Sowing seeds: seed germination and growth of *C. mopane* during drought. *Wastelands News* 19(1):48–50
- Singh G, Kuppusamy V, Rathod T (1999) Performance of multipurpose trees and the associated crops in Indian arid regions. *J Trop For* 15(3):161–170
- Stern N (2007) The Stern Review on the Economics of Climate Change. Public Lecture, London School of Economics, London
- Teskey RO, Hinckley TM (1986) Moisture, effects of water stress on trees. In: Hennessey TC, Dougherty PM (eds) *Stress Physiology and Forest Productivity*. Dordrecht, Boston, Lancaster
- Timberlake J (1996) *C. Mopane*—a tree for all seasons. Sustainable management of indigenous forest in the dry tropics. In: Proc intern conf, Kadoma, Zimbabwe, 28 may–1 June 1996
- Tyree MT, Hammel HT (1972) The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. *J Exp Bot* 23(74):267–282
- Vertovec M, Sakcali S, Ozturk M, Salleo S, Giacomich P, Feoli E, Nardini A (2001) Diagnosing plant water status as a tool for quantifying water stress on a regional basis in Mediterranean drylands. *Ann For Sci* 58(2):113–125
- WBGU (2007) World in transition, climate change as a security risk. WBGU, Berlin

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