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THE *THEMEDA QUADRIVALVIS* TALL-GRASS SAVANNAH OF OMAN AT THE CROSSROAD BETWEEN AFRICA AND ASIA

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Vegetation analysis reveals that the *Themeda quadrivalvis* tall-grass savannah in Oman, southern Arabia, forms a clearly defined belt with strong edaphic and geomorphological characteristics. The newly described association Desmodio gangetico-Themedetum quadrivalvis ass. nov. is interpreted as an impoverished easternmost outlier of the East African savannah.

Keywords. Arabia, endemism, fog-oasis, Oman, phytogeography, phytosociology, southwest monsoon, tall-grass savannah, Themedo-Hyparrhenietea.

INTRODUCTION

The mountains of southern Oman are influenced by the southwest monsoon which creates a tropical fog-oasis in an arid environment. The area is an outstanding example of an island-like refugium: a seasonal cloud-forest in an otherwise arid environment (Kürschner, 1998; Hildebrandt, 2005). The mountain chain in southern Oman and adjacent Yemen has a unique climate which is reflected in a high plant species diversity with high levels of endemism.

These local climatic and geographic factors allow for the survival of subtropical elements in an otherwise unfavourable arid environment. Isolation in space, time and climate has led to the independent development of many taxa, resulting in a high number of endemics (Miller & Nyberg, 1991; White & Léonard, 1991; Patzelt, 2008). The mountains of southern Arabia have recently been added to the list of worldwide biodiversity hotspots as part of the 'Horn of Africa' hotspot (Mittermeier *et al.*, 2005).

Plate tectonics and climate, recent and historic, are the driving forces behind diversity and floristic composition of the *Themeda quadrivalvis* (L.) Kuntze tall-grass savannah in southern Arabia. The relatively late separation of Arabia from Africa and Asia, during the Oligocene, some 10–15 million years BP, allowed for the migration of plants between tropical Africa, southern Arabia and the Indo-Malayan region (Raven & Axelrod, 1974; Mandaville, 1984; Delany, 1989; White & Léonard, 1991; Kürschner, 1998). During the Miocene, when today's separate landmasses

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were still connected, Arabia supported palaeotropical vegetation with swamps and open savannah grassland (Hamilton *et al.*, 1978; Whybrow & McClure, 1981; Mandaville, 1984). During the late Tertiary this vegetation was progressively replaced by more drought-adapted vegetation. Mesic elements of the palaeo-African and palaeo-Indo-Malayan stock could only survive in climatically favourable refugia (Lioubimtseva, 1995; Kürschner, 1998). These refugia in southern Arabia developed during the late Tertiary and early Quaternary through a strong enhancement of the monsoon (Mandaville, 1984; Jolly *et al.*, 1998).

Although the unique vegetation of the 'Dhofar Fog Oasis' (Miller, 1994) has been acknowledged by many authors (e.g. Mandaville, 1977; Radcliffe-Smith, 1980; Miller & Morris, 1988; Miller, 1994), plant community aspects have only recently been investigated (Kürschner *et al.*, 2004). These recent results highlight the significance of this mountain chain where endemic palaeo-African relict plant forest communities, dominated by the endemic *Anogeissus dhofarica* A.J.Scott, are found. In Oman *Themeda* savannahs replace *Anogeissus* forest on plateaus at medium altitudes. They are the tallest grasslands in the country and are restricted to the refugium provided by the southern mountains.

The aims of this study are (i) to identify habitat characteristics, structure, diversity of life forms, biogeographical relationships and the phytosociological classification of the *Themeda quadrivalvis* tall-grass savannah in southern Oman, (ii) to relate species composition to the tall-grass savannah of Yemen and East Africa, and (iii) to correlate biogeographical relationships to Tertiary and Quaternary events.

The study area is located in the fog-affected mountains of southern Oman (Fig. 1). This mountain chain extends some 320 km from the southeastern part of the Al Mahra, Yemen, to southwestern Dhofar, the southern region of the Sultanate of Oman. In Dhofar the mountain chain is built up of three ranges: Jebel Qamar, Jebel Qara and Jebel Samhan. The present study was carried out on Jebel Qamar, situated in the centre of the monsoon-affected area. Jebel Qamar reaches an altitude of 1350 m and forms a steep escarpment to the south, with smaller plateaus between 500 and 800 m. The rock is formed by Cretaceous and Tertiary limestone material, overlaid in many areas with Quaternary scree (Guba & Glennie, 1998). From mid-June to mid-September the area comes under the influence of the southwest monsoon (locally called 'khareef'). During these three months dense fogs build up against the seaward-facing mountains, reaching only a few kilometres inland (Stanley-Price *et al.*, 1988). The low cloudbank cannot rise because of a temperature inversion created by the flow of warm dry air from the inland desert north of the mountain chain. This combination of topography and temperature inversion thus creates a stable fog bank clinging to the sea-exposed slopes. Measurements indicate that fog precipitation during the monsoon amounts to 13 litres/m^2 per day at 0.9 m above the ground and 34–35 litres/m^2 at 4.2 m (Stanley-Price *et al.*, 1988), amounting to two-thirds of the annual precipitation (Hildebrandt, 2005). Unfortunately no long-term climatic data of the study area are available. Climatic data at Qairoon Hariti, situated in the drier part of the mountains, are used for comparison (Fig. 1B).

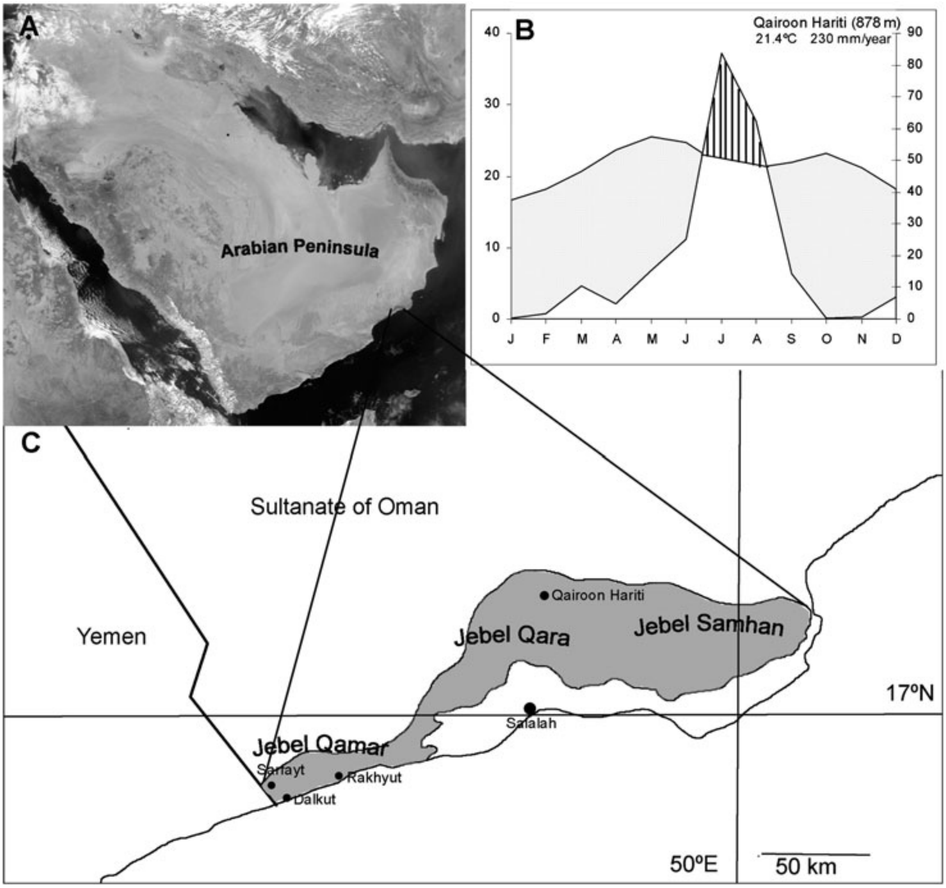

FIG. 1. Location of the mountain chain of southern Oman (A & C) and climatic conditions (B). In B, the left-hand axis is temperature (°C) and the right-hand axis is rainfall (mm).

MATERIALS AND METHODS

The description of the *Themeda* grassland of Oman is based on the traditional Braun-Blanquet cover-abundance scale (Braun-Blanquet, 1964), using the modified scales of Barkman *et al.* (1964) representing the following values: r = solitary, cover < 5%; + = few, less than 1% cover; 1 = few and 1–5% cover; 2m = numerous and cover < 5%; 2a = 6–12% cover; 2b = 13–25% cover; 3 = 25–50% cover; 4 = 51–75% cover; 5 = 76–100% cover. Cover-abundance values are relatively broad subjective classes, and were determined by estimating cover of every single species within the area of the stand. A standard 5-point scale was used to indicate the degree of clumping or gregariousness (sociability) of an individual plant species, obtained as a visual impression, represented by the following values: '1' indicates a shoot growing singly, '2' indicates plants growing in small groups of a few individuals or in small tussocks, '3' indicates small patches, cushions or large tussocks, '4' refers to growing in extensive patches, carpets or broken mats, and '5' indicates plants growing in large mats or pure populations.

The areas of relevés were selected with respect to floristic homogeneity and representation of typical stands. In each relevé and stratum a plant list was established and cover-abundances and sociability were estimated. Fieldwork was carried out in September and November 2003 and September/October 2004 and 2005. The size of the sampling stands varied but was usually 100–200 m^2. The vegetation was sampled in 15 relevés (Table 1). For each relevé a habitat description was recorded which included geographic coordinates, altitude, slope inclination, aspect, height of different strata, plant cover, topographic position and soil characteristics. The study area is located between 16°41′N, 53°06′E and 16°49′N, 53°40′E.

After fieldwork the next stage in this method involved the tabulation of data from similar stands and the synthesis of vegetation units. The final table (Table 1) displays vegetation units which are defined by the presence of particular characteristic species. Finally, the vegetation units under investigation are positioned in the hierarchical floristic system of Braun-Blanquet which requires consideration of the sociological rank and ecological amplitude of each species.

The classification of plant communities at higher syntaxonomic levels in southern Arabia remains difficult as higher levels are not yet known. Therefore, further investigation is needed into which synsystematic rank each species belongs to and how to segregate the higher syntaxa. The syntaxonomic classifications follow the International Code of Phytosociological Nomenclature (Weber *et al.*, 2000).

Family concepts follow APG II (Angiosperm Phylogeny Group, 2003). The taxonomy and nomenclature of the taxa recorded follows Thulin (1993, 1995, 1999, 2006), Miller & Cope (1996), Cope (2007) and Ghazanfar (2003, 2007). Otherwise the most recent taxonomic publications were consulted. Distribution data and chorotypes were mainly compiled from Cope (1985), Miller & Morris (1988), Thulin (1993, 1995, 1999, 2006), Miller & Cope (1996), Ghazanfar (2003, 2007) and Pickering & Patzelt (2008).

For the purposes of this study, an 'endemic species' is defined as a species that occurs in only one country and a 'near-endemic' or 'limited range species' is defined as 'a species which occurs in limited numbers in no more than three countries in Arabia'. For the physiognomic classification, the vegetation structure classification as described in Scholte (2000) has been followed.

Voucher specimens are deposited in the National Herbarium of Oman (ON), and in the Herbarium of Sultan Qaboos University (SQUH). Some duplicates were donated to the Royal Botanic Gardens, Kew (K) and to the Royal Botanic Garden Edinburgh (E).

Within each relevé, 10 soil samples were taken from the surface (0–10 cm depth). The samples were air-dried, mixed and any large stones removed. The soil was then crushed and passed through a 2-mm sieve to remove gravel and debris. The particles not passing the 2-mm sieve were weighed separately for determination of the content of the coarse fragments. The fraction smaller than 2 mm was used for the soil

TABLE 1. The Desmodio gangetico-Themedetum quadrivalvis, a newly described grassland community from southern Arabia. See Materials and Methods for an explanation of the figures

Relevé no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Altitude (m)	552	566	549	574	741	730	720	770	603	770	807	709	622	700	490	
Inclination (°)	5	10	20	5	5	12	5	5	8	4	7	9	5	9	5	
Orientation	SSW	S	S	W	S	S	S	SE	S	SE	S	SSE	SE	SW	E	
Area (m^2)	300	400	100	120	100	160	100	100	200	100	200	220	200	180	400	
Total plant cover (%)	98	100	100	100	85	90	90	90	95	90	85	85	95	95	95	
– Cover trees	–	–	–	–	5	–	2	2	–	–	5	15	5	–	10	
– Cover shrubs	–	5	2	2	2	2	2	5	2	–	10	20	2	5	30	
– Cover herbs	98	95	100	100	95	95	95	90	95	90	70	60	90	95	60	
No. of species	30	29	37	29	28	32	29	28	28	28	36	31	40	43	32	Chorotype
Character species Desmodio gangetico-Themedetum quadrivalvis																
Themeda quadrivalvis (L.) Kuntze	3.5	3.5	5.5	5.5	5.5	5.5	5.5	5.5	5.5	5.5	4.5	5.5	4.5	4.5	2m.3	Indo-Malay.
Setaria pumila (Poir.) Roem. & Schult.	2a.3	2a.3	2m.3	2b.3	2b.3	2a.3	2a.3	2m.3	2a.3	2m.3	2b.3	2a.3	2a.3	2a.3	2b.3	Palaeotrop.-Palaeosubtrop.
Apluda mutica L.	1.3	2a.3	2b.3	2m.3	2a.3	2b.3	3.3	2m.3	2m.3	2m.3	2m.3	2a.3	2a.3	2a.3	2b.3	Indo-Malay.
Desmodium gangeticum (L.) DC.	2m.3	1.3	+.1	+.1	1.1	+.1	1.1	1.1	1.1	1.1	.	+.1	1.1	1.1	+.1	Indo-Malay.
Abelmoschus esculentus (L.) Moench	2a.1	1.3	+.1	+.1	+.1	+.1	1.1	1.1	1.1	+.1	+.1	.	1.1	1.1	+.1	Indo-Malay.
Alysicarpus glumaceus (Vahl) DC.	1.1	2m.3	1.1	1.1	+.1	.	1.1	.	1.1	1.1	.	.	.	1.1	+.1	Somalia-Masai/Sudano-Zamb.
Character species Themedetalia triandrae																
Bothriochloa insculpta (Hochst.) A.Camus	.	.	.	.	.	.	1.1	.	1.1	1.1	.	1.1	.	.	.	Palaeotrop.
Eustachys paspaloides (Vahl) Lanza & Mattei	.	.	2m.3	1.1	.	.	.	.	.	.	.	.	.	.	.	Somalia-Masai/Sudano-Zamb.
Character species Themedo-Hyparrhenietea																
Heteropogon contortus (L.) P.Beauv. ex Roem. & Schult.	.	.	2m.3	2m.3	.	.	2m.3	.	2m.3	.	2m.3	2m.3	.	.	1.3	Pantrop.-Pansubtrop.
Character species Hybantho durae-Anogeissetum dhofaricae (Boscio-Commiphoretea abyssinicae)																
Arthraxon pusillus Bor	2m.3	2m.3	2a.3	2a.3	2m.3	2m.3	2m.3	2m.3	2m.3	2m.3	2m.3	2m.3	2m.3	2m.3	1.1	Endemic

TABLE 1. (*Cont'd*)

Impatiens balsamina L.	+.1	1.3	+.1	.	1.3	1.2	1.2	+.1	.	.	.	.	+.1	+.1	.	Indo-Malay.
Wahlenbergia flexuosa (Hook.f. & Thoms.) Thulin	.	1.3	1.1	2m.3	1.3	.	1.3	1.1	.	1.1	.	.	.	.	1.3	Somalia-Masai/ Indo-Malay.
Maytenus dhofarensis Sebsebe	.	.	.	.	2a.3	.	+.1	+.1	.	.	1.3	2a.3	+.1	.	+.1	Near-Endemic
Allophylus rubifolius (A.Rich.) Engl. var. *rubifolius*	.	1.1	.	.	.	.	.	.	.	.	+.1	+.1	.	.	.	Somalia-Masai/ Sudano-Zamb.
Mitreola petiolata (J.F.Gmel.) Torr. & A.Gray	.	.	.	.	.	.	+.1	.	.	+.1	.	.	+.1	.	.	Pantrop.
Anogeissus dhofarica A.J.Scott	.	.	.	.	.	.	.	.	+.1	.	.	2a.3	.	.	+.1	Near-Endemic
Rungia pectinata Nees	.	.	.	.	.	.	.	.	.	.	2m.3	2m.3	.	.	1.1	Indo-Malay.
Ruttya fruticosa Lindau	.	.	.	.	+.1	.	+.1	.	.	.	.	.	.	.	.	Somalia-Masai
Launaea crassifolia (Balf.f.) C.Jeffrey	.	.	.	.	.	.	.	.	.	.	.	+.1	.	1.1	.	Somalia-Masai
Blepharispermum hirtum Oliver	.	.	+.1	.	.	.	.	.	.	.	.	.	.	.	.	Near-Endemic
Exacum arabicum Thulin	.	.	.	.	.	.	.	.	.	.	.	.	.	1.1	.	Near-Endemic
Character species Boscio-Commiphoretalia and Boscio-Commiphoretea abyssinicae																
Commiphora gileadensis (L.) C.Christ.	.	.	+.1	.	+.1	+.1	.	+.1	.	+.1	+.1	+.1	1.1	1.1	.	Somalia-Masai
Cyphostemma ternatum (Forssk.) Desc.	.	.	.	.	+.1	+.1	+.1	.	.	.	.	+.1	+.1	+.1	.	Somalia-Masai
Teramnus repens (Taub.) Baker f. subsp. *gracilis* (Chiov.) Verd.	1.1	.	1.1	1.1	.	.	.	+.1	.	+.1	.	.	.	.	.	Somalia-Masai/ Sudano-Zamb.
Flueggea virosa (Roxb. ex Willd.) Royle	.	.	+.1	.	.	.	.	.	.	.	.	.	.	+.1	.	Palaeotrop.
Commiphora kua (J.F.Royle) Vollesen	.	.	+.1	.	.	.	.	.	.	.	.	.	.	.	+.1	Somalia-Masai/ Sudano-Zamb.
Rhynchosia minima (L.) DC. var. *minima*	.	.	.	.	.	.	.	.	.	.	.	.	.	+.1	1.1	Pantrop.
Character species Oleo-Juniperetalia procerae (Juniperetea procerae)																
Jasminum grandiflorum subsp. *floribundum* (Fresen.) P.S.Green	.	.	.	.	.	.	.	.	.	.	1.3	1.1	+.1	1.1	+.1	Somalia-Masai
Olea europaea subsp. *cuspidata* (Wall. ex G.Don) Cif.	.	.	.	.	.	.	.	.	.	.	1.2	+.1	+.1	.	+.1	Pluriregional
Rhamnus staddo A.Rich.	.	.	.	.	.	.	.	.	.	.	1.1	.	.	1.1	.	Somalia-Masai

TABLE 1. (*Cont'd*)

Character species Pistachio-Eucleetalia schimperi (Hyperico-Rhamnetea)																
Dodonaea viscosa (L.) Jacq.	.	1.3	1.1	.	.	.	.	.	.	.	.	.	.	.	2b.3	Pantrop.-Pansubtrop.
Euclea schimperi (A.DC.) Dandy	.	.	.	.	.	.	.	.	.	.	+.1	1.1	.	.	.	Somalia-Masai/Sudano-Zamb.
Pavetta longiflora Vahl	.	.	.	.	.	.	.	.	.	.	.	+.1	.	.	.	Regional-Endemic
Grazing indicators																
Senna obtusifolia (L.) H.S.Irwin & Barneby	2a.3	2a.3	1.1	2m.3	2a.2	1.1	1.2	+.1	1.1	+.1	2a.3	2a.3	1.1	1.1	2b.3	Pantrop.
Crotalaria retusa L.	2a.3	1.3	.	.	2a.2	1.1	.	+.1	2a.3	+.1	2a.3	1.3	1.1	1.1	1.1	Pantrop.
Triumfetta pentandra A.Rich.	2b.3	2a.3	2m.3	2m.3	.	2a.3	2a.3	2a.3	2m.3	2m.3	.	.	2a.3	.	2a.3	Somalia-Masai/Indo-Malay.
Solanum incanum L.	.	.	.	.	+.1	.	.	+.1	.	.	+.1	+.1	+.1	+.1	+.1	Somalia-Masai/Saharo-Sindian
Bidens biternata (Lour.) Merr. & Sherff	.	.	+.1	.	.	.	.	.	.	.	.	.	.	+.1	.	Palaeotrop.
Companions																
Arthraxon micans (Nees) Hochst.	2b.3	2a.3	1.1	2m.3	2a.3	2b.3	2a.3	1.1	2a.3	2m.3	2m.3	2m.3	2b.3	2b.3	2m.3	Somalia-Masai/Indo-Malay.
Orthosiphon pallidus Royle ex Benth.	+.1	1.3	1.1	.	.	1.1	1.1	+.1	.	+.1	1.1	.	+.1	1.3	1.1	Palaeotrop.
Vigna radiata (L.) Wilczek	2m.3	1.1	.	+.1	1.2	1.1	1.1	+.1	1.1	1.1	.	.	.	1.1	1.1	Pantrop.
Alysicarpus vaginalis (L.) DC.	2m.3	2m.3	1.1	2m.3	2m.3	2m.3	.	1.1	1.1	+.1	.	.	2m.3	.	.	Palaeotrop.
Pimpinella schweinfurthii Asch.	1.1	.	2m.3	.	.	.	.	1.3	1.3	1.3	1.3	2m.3	2m.3	1.1	1.1	Saharo-Sindian
Anagallis arvensis L.	+.1	.	.	+.1	.	+.1	1.1	1.1	+.1	+.1	.	.	.	+.1	.	Cosmopol.
Oldenlandia corymbosa L.	2m.3	.	2m.3	2m.3	2m.3	2m.3	.	2m.3	2m.3	.	2m.3	.	.	.	.	Pantrop.
Buchnera hispida Buch.-Ham. ex D.Don	.	1.1	.	1.1	+.1	.	.	+.1	+.1	+.1	.	.	+.1	1.1	.	Somalia-Masai
Euphorbia indica Lam.	2m.3	2m.3	.	2m.3	2m.3	.	.	.	2m.3	2m.3	.	.	.	.	1.2	Indo-Malay.
Viola cinerea Boiss. var. *stocksii* (Boiss.) Becker	1.3	.	2m.3	+.1	1.3	1.3	1.3	.	.	1.3	.	.	.	.	.	Somalia-Masai/Saharo-Sindian
Canscora concanensis C.B.Clarke	.	.	.	.	1.1	.	1.1	1.1	1.1	1.1	.	.	2m.3	1.1	.	Indo-Malay.
Cucumis sativus L.	.	+.1	.	.	+.1	.	.	.	+.1	.	.	+.1	+.1	+.1	.	Pantrop.-Pansubtrop.

TABLE 1. (*Cont'd*)

Digitaria stricta Roth ex Roem. & Schult.	.	2m.3	.	1.1	.	2m.3	2m.3	.	1.1	.	.	.	.	.	+.1	Indo-Malay.
Dichanthium annulatum (Forssk.) Stapf	1.1	2m.3	.	2a.3	.	1.1	1.1	.	.	.	.	.	.	.	.	Palaeotrop.
Convolvulus prostratus Forssk.	+.1	.	.	+.1	.	+.1	.	.	.	.	.	.	.	1.1	1.2	Somalia-Masai/ Saharo-Sindian
Blumea mollis (D.Don) Merr.	.	+.1	.	.	.	+.1	.	.	.	.	1.2	.	1.1	.	1.3	Pantrop.- Pansubtrop.
Brachiaria eruciformis (Sm.) Griseb.	.	.	.	.	.	.	1.1	1.1	1.1	.	+.1	.	.	1.1	.	Pluriregional
Fimbristylis bisumbellata (Forssk.) Bubani	.	+.1	1.1	.	.	.	.	.	.	.	.	.	2m.3	2m.3	.	Palaeotrop.
Adenium obesum (Forssk.) Roem. & Schult.	.	+.1	.	.	.	.	.	.	+.1	.	1.1	+.1	.	.	.	Somalia-Masai/ Sudano-Zamb.
Cyperus squarrosus L.	.	.	.	.	.	1.3	.	1.2	.	.	.	.	1.1	1.1	.	Pantrop.
Woodfordia uniflora (A.Rich.) Koehne	.	.	.	.	.	.	.	.	+.1	.	+.1	+.1	.	1.1	.	Somalia-Masai
Brachiaria lata (Schumach.) C.E.Hubb.	1.1	2m.3	.	.	1.1	.	.	.	.	.	.	.	.	.	.	Somalia-Masai/ Sudano-Zamb.
Centaurea dhofarica Baker	1.1	.	+.1	1.1	.	.	.	.	.	.	.	.	.	.	.	Near-Endemic
Brachiaria ramosa (L.) Stapf	1.1	.	.	.	.	1.1	.	.	.	.	.	.	1.1	.	.	Somalia-Masai/ Indo-Malay.
Plectranthus barbatus Andrews	.	.	1.1	.	.	.	.	.	.	.	1.1	.	.	+.1	.	Palaeotrop.
Commelina cf. *albescens* Hassk.	.	.	.	.	1.3	1.2	.	.	.	.	.	.	.	1.1	.	Somalia-Masai/ Sudano-Zamb.
Adiantum lunulatum Burm.f.	.	.	.	.	1.3	.	+.2	.	.	.	.	.	.	+.1	.	Pantrop.- Pansubtrop.
Lobelia heyniana Roem. & Schult.	.	.	.	.	.	1.1	.	.	1.1	.	.	.	1.1	.	.	Indo-Malay.
Remusatia vivipara (Roxb.) Schott	.	.	.	.	.	.	.	.	.	.	1.3	1.3	1.1	.	.	Palaeotrop.
Setaria intermedia Roem. & Schult.	+.1	.	.	.	.	.	.	.	.	.	.	.	2m.3	.	.	Somalia-Masai/ Indo-Malay.
Convolvulus arvensis L.	+.1	.	1.1	.	.	.	.	.	.	.	.	.	.	.	.	Cosmopol.
Tephrosia humilis Guill. & Perr.	.	+.1	1.1	.	.	.	.	.	.	.	.	.	.	.	.	Somalia-Masai/ Indo-Malay.
Hackelochloa granularis (L.) Kuntze	.	.	2m.1	+.1	.	.	.	.	.	.	.	.	.	.	.	Pantrop.
Hermannia paniculata Franch.	.	.	+.1	1.1	.	.	.	.	.	.	.	.	.	.	.	Somalia-Masai

TABLE 1. (*Cont'd*)

Polygala tinctoria Vahl	.	.	+.1	.	.	.	.	.	.	.	.	+.1	.	.	.	Regional-Endemic
Chrysopogon macleishii Cope	.	.	.	.	.	1.1	.	+.1	.	.	.	.	.	.	.	Endemic
Dimeria ornithopoda Trin.	.	.	.	.	.	1.3	.	.	.	1.3	.	.	.	.	.	Indo-Malay.
Dorstenia foetida (Forssk.) Schweinf.	.	.	.	.	.	1.3	.	.	.	.	2m.3	.	.	.	.	Somalia-Masai
Gladiolus candidus (Rendle) Goldblatt	.	.	.	.	.	.	+.1	.	.	1.1	.	.	.	.	.	Somalia-Masai
Dyschoriste dalyi A.G.Mill.	.	.	.	.	.	.	+.1	.	.	+.1	.	.	.	.	.	Endemic
Gomphocarpus fruticosus subsp. *setosa* (Forssk.) Goyder & Nicholas	.	.	.	.	.	.	.	.	.	.	1.1	+.1	.	.	.	Pluriregional
Arundinella pumila (Hochst. ex A.Rich.) Steud.	.	.	.	.	.	.	.	.	.	.	1.3	.	2m.3	.	.	Somalia-Masai/ Indo-Malay.
Negripteris sciona (Chiov.) Pic.-Serm.	.	.	.	.	.	.	.	.	.	.	2m.3	.	.	1.1	.	Somalia-Masai/ Sudano-Zamb.
Rhus somalensis Engl.	.	.	.	.	.	.	.	.	.	.	+.1	.	.	.	+.1	Somalia-Masai
Ficus sycomorus L.	.	.	.	.	.	.	.	.	.	.	.	1.1	+.1	.	.	Pluriregional
Anagallis pumila Sw.	.	.	.	.	.	.	.	.	.	.	.	.	1.1	2m.3	.	Somalia-Masai/ Saharo-Sindian
Cyperus alulatus J.Kern	.	.	.	.	.	.	.	.	.	.	.	.	1.1	1.1	.	Somalia-Masai/ Sudano-Zamb.

Additional species:
A 2: *Senra incana* Cav. +.1; *Tripogon leptophyllus* (A.Rich.) Cufod. 1.3. **A 8**: Gramineae indet +.1. **A 22**: *Abelmoschus manihot* (L.) Medik. 1.1. **A 24**: *Orobanche dhofarensis* M.J.Y.Foley 1.3. **A 25**: *Andrachne aspera* Spreng. 1.2; *Carissa spinarum* L. +.1; *Corchorus trilocularis* L. +.1; *Cordia crenata* Delile subsp. *crenata* +.1. **A 51**: *Heliotropium longiflorum* (Hochst. ex A.DC.) Jaub. & Spach +.1; *Nicandra physalodes* Gaertn. +.1. **A 52**: *Schizachyrium brevifolium* (Sw.) Nees ex Büse 1.1. **A 54**: *Eclipta prostrata* (L.) L. r.1; *Eragrostis viscosa* (Retz.) Trin. 2m.3; *Cyperus longus* L. +.1; *Ficus vasta* Forssk. +.1; *Indigofera tinctoria* L. +.1. **A 55**: *Achyranthes aspera* L. +.1; *Ceropegia bulbosa* Roxb. +.1; *Aloe praetermissa* McCoy & Lavranos +.1; *Scrophularia arguta* Aiton 2m.3. **A 73**: *Cleistachne sorghoides* Benth. +.1; *Digitaria ciliaris* (Retz.) Koeler 1.1; *Vernonia cinerea* (L.) Lees 1.1. **A 74**: *Enicostemma axillare* (Lam.) A.Raynal 1.1; *Sida ovata* Forssk. +.1.

analysis. Soil texture was determined according to Benzler *et al.* (1982). Soil-water extracts (1:5) were prepared for measurement of pH. To test carbonate content, hydrochloric acid was added to 5 g of sieved soil (air-dried soil fraction < 2 mm) on a watch glass. The carbonate content was measured on the basis of the intensity and time of effervescence (Benzler *et al.*, 1982).

Results

Soil, vegetation structure and species composition of the Arabian Themeda *grassland*

The *Themeda* grassland (Fig. 2) forms a belt on the gentle seaward slopes with a width of about 3–5 km and is restricted to a narrow altitudinal range of 500–800 m. The grassland is found almost exclusively on south-facing slopes with an inclination of 4–20°. The soil texture is silty clay with a pH between 6.4 and 6.7; carbonate content is low. The soil type is a vertisol. During the dry season the soil becomes extraordinarily hard and is divided into rough polygons and prisms; wide cracks develop to a depth of 50 cm or more. The cracks close during the monsoon when the clay minerals swell. Skeletal rock comprises up to 10% of the surface of the relevés.

FIG. 2. Typical aspect of the *Themeda quadrivalvis* grassland in southern Oman.

The *Themeda* grassland is rich in species (112 taxa, mean species number/relevé = 32; Table 1). Twelve species (11%) found in the grassland are endemic, near-endemic or regionally endemic (Table 3). Both structurally and floristically, the grassland community is characterised by the dominance of the annual grass *Themeda quadrivalvis*, which can reach 2.5 m in height and often occupies more than 70% of the total cover.

In Arabia *Themeda quadrivalvis* is restricted to southern Oman and southeastern Yemen, whereas *Themeda triandra* Forssk. is found along the western mountain chain in Yemen and also in Soqotra (Cope, 2007). *Themeda quadrivalvis* was also recorded from Soqotra in the 19th century but has not been seen since (Miller & Morris, 2004). Globally the annual *Themeda quadrivalvis* has a much more restricted distribution, whereas the perennial *T. triandra* is distributed throughout the tropical and subtropical Old World and, in many places, is regarded as a problematic species.

In Oman *Themeda quadrivalvis* and other grasses are associated with groups of trees and shrubs mainly composed of the endemics *Anogeissus dhofarica* and *Maytenus dhofarensis* Sebsebe, and the evergreen *Olea europaea* subsp. *cuspidata* (Wall. ex G.Don) Cif. The herb and shrub layer is characterised by three distinct strata. The upper stratum is dominated by the tall annual *Themeda quadrivalvis*. Shorter grasses (e.g. *Apluda mutica* L., *Setaria pumila* (Poir.) Roem. & Schult.) form an intermediate stratum up to 80 cm tall. The lowest stratum consists mainly of small annual grasses and therophytes up to 15 cm tall. Therophytes clearly dominate the grassland (50%), but shrubby chamaephytes (19%), hemicryptophytes (11%) and phanerophytes (16%) are common as well. Geophytes play a minor role (3%). Rocks provide a more sheltered habitat and thus enable some perennials to grow, such as the stem succulent *Dorstenia foetida* (Forssk.) Schweinf.

TABLE 2. Percentage of different chorotypes in the *Themeda quadrivalvis* grassland in different strata, reflecting the phytogeographical affinities

	Tree layer (n = 7)	Shrub layer (n = 18)	Herb and dwarf shrub layer (n = 87)	All layers (n = 112)
Endemic/Near-Endemic/ Regional-Endemic	28.5	17	7	10
Somalia-Masai	28.5	33	8	13
Indo-Malayan	–	–	16	12.5
Biregionals: Somalia-Masai/ Sudano-Zambesian	14.5	17	9	11
Biregionals: Somalia-Masai/ Indo-Malayan	–	5.5	17	14
Biregionals: Somali-Masai/ Saharo-Sindian	–	5.5	4.5	4.5
Palaeotropical	–	5.5	11.5	10
Pantropical	–	5.5	21	17
Pluriregional	28.5	11	6	8

TABLE 3. Range-restricted species in the *Themeda quadrivalvis* grassland

Species	Family	Chorotype
Dyschoriste dalyi A.G.Mill.	Acanthaceae	Endemic
Aloe praetermissa McCoy & Lavranos	Asphodelaceae	Endemic
Blepharispermum hirtum Oliver	Asteraceae	Near-Endemic
Centaurea dhofarica Baker	Asteraceae	Near-Endemic
Maytenus dhofarensis Sebsebe	Celastraceae	Near-Endemic
Anogeissus dhofarica A.J.Scott	Combretaceae	Near-Endemic
Exacum arabicum Thulin	Gentianaceae	Near-Endemic
Arthraxon pusillus Bor	Poaceae	Endemic
Chrysopogon macleishii Cope	Poaceae	Endemic
Polygala tinctoria Vahl	Polygalaceae	Regional-Endemic
Pavetta longiflora Vahl	Rubiaceae	Regional-Endemic
Orobanche dhofarensis M.J.Y.Foley	Scrophulariaceae	Endemic

The yearly cycle of plant activity is strongly correlated with the monsoon precipitation and corresponding changes in available moisture. As soon as the first fog arrives at the end of June, the annual species germinate and deciduous perennials sprout their first leaves. Most of the annuals set seed at the end of the humid season in October/November. The grassland is used for grazing of livestock, mainly after the monsoon fogs have lifted. Grazing indicators are common and conspicuous non-palatable palaeotropical and pantropical weeds can reach high cover values. The chorotype analysis indicates a community with strong affinities to xerotropical and subtropical grasslands of Yemen and East Africa as well as subtropical Southeast Asia (Table 2).

The phytosociological analysis of the community has led to the description of a new plant community, the Desmodio gangetico-Themedetum quadrivalvis (see Table 1). Characteristic species are the grasses *Themeda quadrivalvis*, *Setaria pumila* and *Apluda mutica*, and the herbs *Desmodium gangeticum* (L.) DC., *Abelmoschus esculentus* (L.) Moench and *Alysicarpus glumaceus* (Vahl) DC. The Desmodio-Themedetum is relatively uniformly developed but towards the escarpment rim trees and shrubs become more dominant, indicated by species of the sclerophyllous evergreen *Anogeissus dhofarica* woodlands (relevés nos. 11–15 in Table 1).

DISCUSSION

Environmental determinants

A total of 112 taxa were found in the *Themeda* grassland on Jebel Qamar. As the country's total flora comprises c.1200 species (Miller & Cope, 1996), 9.5% of the total flora is represented in the grassland, a high percentage.

The geographically closest tall-grass savannah dominated by *Themeda* sp. is located in Yemen, including Soqotra, and Ethiopia (Pichi-Sermolli, 1957; White, 1983; Friis, 1992; Miller & Morris, 2004; Suttie *et al.*, 2005; World Wildlife Fund, 2010). A comparison with phytosociological studies from East African data extracted from Lebrun (1947), Knapp (1973), Schmidt (1975a, 1975b) and White (1983) reveals a number of linking species: *Eustachys paspaloides* (Vahl) Lanza & Mattei, *Heteropogon contortus* (L.) P.Beauv. ex Roem. & Schult. and *Bothriochloa insculpta* (Hochst.) A.Camus.

Grassland dominated by *Themeda quadrivalvis* is also found on the outer escarpment mountains of southeastern Yemen (A. G. Miller, pers. comm.). In Yemen, *Heteropogon contortus*, *Bothriochloa insculpta* and *Eustachys paspaloides* are found in similar grassland vegetation (A. G. Miller, pers. comm.). Further studies are required to investigate the *Themeda* grasslands on the monsoon-affected mountains of Soqotra and on the escarpment mountains of Yemen to elucidate their relationship with the *Themeda* grassland of southern monsoon-affected Oman.

Compared with the *Themeda triandra* savannah in East Africa, however, species diversity in southern Arabia is far lower. For example, Schmidt (1975b) reported at least 260 taxa from Tanzania. Studies of the *Themeda* grasslands of Ethiopia (Suttie *et al.*, 2005) reveal that species diversity seems to be higher than in the *Themeda quadrivalvis* grassland of Oman. The *Themeda* grassland of Oman is impoverished in species compared with the African *Themeda* savannah.

Low shrub and tree cover in savannah vegetation on vertisol has been explained by wetness of the soil and resulting low levels of oxygen during the monsoon with correspondingly extreme shrinkage and hardness in the dry season (Schmidt, 1975b). Therefore, the dominant life forms are therophytes, which can withstand these severe environmental conditions (Huntley, 1982; Menault, 1983). Higher cover and abundance of trees and shrubs on steeper slopes towards the escarpment rim can be explained by better drainage conditions.

The use of the *Anogeissus* forest for browsing and the clearing of forest to provide pastures have a long history in Dhofar. The grassland of Oman has supported pastoral communities for thousands of years without excessive overgrazing except in the last three decades (Miller & Morris, 1988). In recent years, high densities of grazers, principally cattle and camels, and changes towards the communities becoming more sedentary have had a severe effect, leading to high cover values of unpalatable herbs, such as *Crotalaria retusa* L. and *Nicandra physalodes* (L.) Gaertn.

Phytogeographical affinities of the Themeda quadrivalvis *grassland*

Phytogeographically the vegetation of the monsoon-affected mountains in Dhofar marks the easternmost extent of the Somalia-Masai regional centre of endemism (Léonard, 1988; White & Léonard, 1991; Ghazanfar, 1992; Kürschner, 1998). The close floristic relationships between East Africa and southern Arabia are evident from the 24% of species which belong to the Somalia-Masai and Sudano-Zambesian chorotype (Table 2). These palaeotropical African floristic elements reach their easternmost limit in Dhofar, whereas the Indo-Malayan species are at their westernmost limit in southern Arabia.

Clayton & Cope (1980) indicated that the grasses in southern Arabia have strong links to Asia. This is well supported by the present study. Only a few Saharo-Sindian geoelements are found in the *Themeda* grassland, although the mountain chain is bordered to the north by a desert dominated by Saharo-Sindian species. The absence of these taxa is due to the humid site conditions during the monsoon season which restricts Saharo-Sindian elements. The palaeotropical species clearly reflect the former land connection of Arabia with Africa and Asia. The pantropical and pluriregional species are mainly weedy and ruderal species, indicating recent human influence.

The occurrence of endemic and near-endemic species in the *Themeda* grasslands underlines the importance of the monsoon-influenced mountains of southern Arabia as a refuge area, representing a regional centre of endemism (Table 3). The 'Dhofar Fog Oasis' is a centre of species richness (Miller & Nyberg, 1991; Miller, 1994) and these centres usually coincide with centres of endemism (Crisp *et al.*, 2001). Recent work highlights the concentration of range-restricted and rare and threatened species in southern Oman where a total of 145 range-restricted species, representing 12.1% of the total flora, are found (Patzelt, 2008). Endemic and near-endemic species occur quite frequently in the grassland and are relatively widespread. These species are, per definition, rare, and therefore potentially threatened on a global level (Myers *et al.*, 2000). The *Themeda* grassland is thus an important habitat for the survival of species with restricted distribution and requires greater conservation effort.

Phytosociological classification reveals the position within the East African Themedo-Hyparrhenietea

Classification at the community level has so far not been performed on Arabian grasslands (Deil & Al Gifri, 1998) and only on small portions of the African savannah (e.g. in East Africa by Lebrun, 1947; Troupin, 1966; Leippert, 1968; Quezel, 1969; Schmidt, 1975b) and South Africa (reviewed in Cowling *et al.*, 1997). No detailed analysis at community level from the grasslands on the Indian subcontinent has so far been undertaken (Misra, 1983).

On the basis of close floristic relationships, the *Themeda* grasslands in Oman are interpreted as the easternmost outliers of the African *Themeda* tall-grass savannah. Stand number 3 represents the typus stand of the Desmodio gangetico-Themedetum quadrivalvis ass. nov.

Knapp (1965) combined all East and South African tall-grass savannah types into the class Themedo-Hyparrhenietea Knapp 1965. The analysis of the herbaceous layer of the *Themeda quadrivalvis* grasslands from Dhofar reveals its position in this class (Knapp, 1965, 1968), with *Heteropogon contortus* as a characteristic species of the class and *Bothriochloa insculpta* and *Eustachys paspaloides* as characteristic species of the order Themedetalia triandrae sensu Lebrun 1947. Classification within an alliance still remains unclear and the relationship of the grasslands dominated by *Themeda quadrivalvis* to the grasslands dominated by *T. triandra* requires further study.

Besides taxa of the tall-grass savannah, species of other phytosociological classes are important for the characterisation of the Dhofar grassland. Further species that always occur are characteristic of the Hybantho durae-Anogeissetum dhofaricae Kürschner *et al.* 2004, a drought-deciduous forest community of the Boscio-Commiphoretea abyssinicae (= *Acacia–Commiphora* drought-deciduous woodland – Zohary, 1973). In East Africa these are often replaced by evergreen shrub communities of the Pistachio-Eucleetalia schimperi (Gillett, 1941; Hemming, 1966). Montane African-Arabian forest communities of the Oleo-Juniperetalia procerae (Pichi-Sermolli, 1957; Knapp, 1965, 1968, 1973; White, 1983; König, 1987) are restricted to forested patches within the grassland.

In Dhofar, the *Themeda* grassland is in direct contact with two different forest communities of the Boscio-Commiphoretea abyssinicae. On the south-facing sea-exposed side the gentle slopes covered in grassland are suddenly replaced by *Anogeissus* forest on steep, almost perpendicular, escarpments. On the north-facing slopes, beyond the monsoon precipitation, the grassland is replaced quite abruptly by drought-deciduous *Acacia–Commiphora* woodland. Many of the grassland species occur as marginal intruders on edaphically shallow sites in the *Anogeissus* forest but are absent from the dry woodland.

Thus, most grassland species are 'borrowed' from adjacent forests with similar moisture conditions and were able to invade open habitats created after clearing of the forests. This is in agreement with the suggested origin of most African savannah grass species (White, 1978). It is therefore suggested that the *Themeda* grassland in Oman results from anthropogenic activities. A similar explanation is suggested for the grassland in open areas in *Anogeissus* forest in southeastern Yemen (Hauf), situated within the same geographic region (Kürschner *et al.*, 2004). An anthropogenic origin has also been suggested for grassland-fragments in Yemen with *Heteropogon contortus*, *Bothriochloa insculpta* and *Themeda triandra* (Deil & Müller-Hohenstein, 1985).

As all the mountains of southern Arabia are affected by the southwest and northeast monsoons, it is highly likely that the newly described association will also be found within *Anogeissus* forest on Ras Fartak west of Hauf in Yemen and may also extend into Soqotra (A. G. Miller, pers. comm.).

Conservation status

Within the grasslands there are 12 taxa, representing 11% of the total within the grasslands, which require a high conservation priority (Patzelt, 2008) in order to maintain the current high plant diversity. Overgrazing has already led to a degeneration of the plant community and an invasion of many unpalatable weeds which now dominate in severely overgrazed areas. In many areas in Dhofar the grasslands are so heavily grazed that the grasses no longer reach reproductive maturity.

Although overgrazing is the major direct threat to this plant community it is clear that without the involvement and cooperation of local people there can be little hope for future conservation efforts. The inclusion of local people offers the best prospect for the control of grazing pressure and for exploration of new practices and new uses of rangelands. It is therefore essential that efforts be made to promote a policy of sustainable development and conservation of the environment to ensure a good standard of living for local people while conserving the native flora.

Principal Results

1 Isolation in space, time and climate has led to a unique and endemic plant community, the Desmodio gangetico-Themedetum quadrivalvis ass. nov., which is found exclusively in the monsoon-affected mountains of Dhofar and probably also in adjacent Yemen.
2 This annual grassland is interpreted as the easternmost outlier of the East African tall-grass savannah in the class Themedo-Hyparrhenietea Knapp 1965.
3 Taxa of xeric-African, mesic-African and mesic-tropical Asian origin indicate the importance of southern Arabia as a migration link during the Tertiary.
4 The seasonal fog-oasis conditions in an otherwise arid environment offer a refuge area for palaeotropical mesic elements.
5 The tall-grass savannah in Oman is an important habitat for endemic and near-endemic species and thus deserves further investigation and greater conservation effort.

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