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Artigo

PLANT COMMUNITIES OF NAMIBE SALTMARSHES (SOUTHWEST OF ANGOLA)

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ABSTRACT – This work constitutes the first phytosociological analysis of saltmarshes on the Angolan coast. Sixty-five relevés were carried out resulting in the description of six new plant associations. These saltmarshes are characterized by a lower floristic richness when compared to the Holarctic saltmarshes. Eighteen taxa were identified, some of them succulent. Saltmarshes occur from the mouth of the Cunene River to the Cuanza River, although in this last part they are already very impoverished. In the Cuanza river, saltmarshes occupy only a narrow strip in the inner sector of the mangroves in contact with continental ecosystems and are often made up of just one taxon, *Sarcocornia natalensis* subsp. *affinis*. Mangroves reach their southern limit in the city of Lobito, although they are almost extinct there. The occurrence and distribution of saltmarshes are affected by the Cold Benguela Current, that influences the west coast of Africa between Cabo da Boa Esperança and Benguela. The height of the saltmarsh's platforms colonized by halophyte, sub-halophyte or halotolerant plants determines the flooding period and thus the plant community's floristic composition. Soil granulometry also plays an important role in the spatial organization of

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plant communities. One of the main originalities of Angolan saltmarshes is the predominance of fine sandy or sandy-loam soil texture as a consequence of the proximity of the Namibe desert. The PCA segregated the different plant communities described.

Keywords: Saltmarshes; phytosociology; PCA; vegetation.

RESUMO – COMUNIDADES VEGETAIS DOS SALGADOS DO NAMIBE (SUDOESTE DE ANGOLA). Este trabalho constitui a primeira análise fitossociológica de sapais da costa angolana. Sessenta e cinco inventários foram realizados resultando na descrição de seis novas associações de plantas. Estes sapais são caracterizados por uma menor riqueza florística quando comparadas aos sapais holárticos. Dezoito táxons foram identificados, alguns deles suculentos. Os sapais ocorrem desde a foz do rio Cunene até ao rio Cuanza, embora nesta última parte já estejam muito empobrecidos. No rio Cuanza, os sapais ocupam apenas uma faixa estreita no setor interno dos mangais em contato com os ecossistemas continentais e geralmente são constituídos por um único táxon, *Sarcocornia natalensis* subsp. *affinis*. Os mangais atingem seu limite sul na cidade de Lobito, embora estejam quase extintos. A ocorrência e distribuição dos sapais são afetados pela Corrente Fria de Benguela, que influencia a costa oeste da África entre o Cabo da Boa Esperança e Benguela. A altura das plataformas do sapal colonizadas por plantas halófitas, subhalófitas ou halotolerantes determina o período de inundação e, portanto, a composição florística das comunidades vegetais. A granulometria do solo também desempenha um papel importante na organização espacial das comunidades de plantas. Uma das principais originalidades dos sapais angolanos é o predomínio de solos de textura arenosa fina ou franco-arenosa, em consequência da proximidade com o deserto do Namibe. A ACP segregou as diferentes comunidades de plantas descritas.

Palavras-chave: Sapais; fitossociologia; ACP; vegetação.

RÉSUMÉ – COMMUNAUTÉS VÉGÉTALES DES MARAIS SALÉS DE NAMIBE (SUD-OUEST D'ANGOLA). Ce travail constitue la première analyse phytosociologique des marais salants de la côte angolaise. Soixante-cinq relevées ont été réalisés aboutissant à la description de six nouvelles associations végétales. Ces marais salants se caractérisent par une richesse floristique plus faible que les marais salants holarctiques. Dix-huit taxons ont été identifiés, certains d'entre eux succulents. Les marais salants se trouvent dès l'embouchure de la rivière Cunene à la rivière Cuanza, bien que dans cette dernière partie ils soient déjà très appauvris. Dans la rivière Cuanza, les marais salants n'occupent qu'une bande étroite dans le secteur intérieur des mangroves en contact avec les écosystèmes continentaux et sont souvent constitués d'un seul taxon, *Sarcocornia natalensis* subsp. *affinis*. Les mangroves atteignent leur limite sud dans la ville de Lobito bien qu'elles y soient presque éteintes. La présence et la distribution des marais salants sont affectées par le courant froid de Benguela qui influence la côte ouest de l'Afrique entre le Cabo da Boa Esperança et Benguela. La hauteur des plates-formes du marais salé colonisées par des plantes halophytes, sous-halophytes ou halotolérantes détermine la période d'inondation et donc la composition floristique des communautés végétales. La granulométrie du sol joue également un rôle important dans l'organisation spatiale des communautés végétales. L'une des principales originalités des marais salants angolais est la prédominance de sols de texture sableuse ou sablo-limoneuse en raison de la proximité du désert de Namibe. L'ACP a séparé les différentes communautés végétales décrites.

Mot clés: Marais salés; phytosociologie; ACP; végétation.

RESUMEN – COMUNIDADES VEGETALES DE LAS MARISMAS DE NAMIBE (SUROESTE DE ANGOLA)**.** Este trabajo constituye el primer análisis fitosociológico de las marismas del litoral angoleño. Se realizaron sesenta y cinco inventarios que dieron como resultado la descripción de seis nuevas asociaciones de plantas. Estas marismas salinas se caracterizan por una menor riqueza florística en comparación con las marismas salinas de Holarctic. Se identificaron dieciocho taxones, algunos de ellos suculentos. Las marismas se dan desde la desembocadura del río Cunene hasta el río Cuanza, aunque en este último tramo ya están muy empobrecidas. En el río Cuanza, las marismas ocupan solo una franja estrecha en el sector interior de los manglares en contacto con los ecosistemas continentales y, a menudo, están formadas por un solo taxón, *Sarcocornia natalensis* subsp. *affinis*. Los manglares alcanzan su límite Sur en la ciudad de Lobito, aunque allí están casi extintos. La ocurrencia y distribución de las marismas se ven afectadas por la Corriente Fría de Benguela, que influye en la costa occidental de África entre Cabo da Boa Esperança y Benguela. La altura de las plataformas de la marisma colonizada por plantas halófitas, subhalófitas o halotolerantes determina el período de inundación y, por tanto, la composición florística de las comunidades vegetales. La granulometría del suelo también juega un papel importante en la organización espacial de las comunidades vegetales. Una de las principales originalidades de las marismas angoleñas es el predominio de la textura del suelo de arena fina o franco-arenosa como consecuencia de la proximidad del desierto de Namibe. El ACP segregó las diferentes comunidades vegetales descritas.

Palabras clave: Marismas; fitosociología; ACP; vegetación.

I. INTRODUCTION

In the biosphere, amphibious and coastal tidal mudflat ecosystems are formed by saltmarsh and mangrove habitats. The latter consist of a shrubby or arboreal, helo-halophytic vegetation formation, characteristic of the low-lying muddy areas, such as coastal swamps or lagoon banks, within intertropical environments. Mangrove species are physiologically and morphologically adapted to the amphibian eu-haline environment, withstanding high osmotic pressures and developing aerial root systems and pneumatophores (Moreira, 1984). Unlike mangroves, marshes don't have arboreal species and colonise mainly temperate zones in the western part of the continents, under the influence of cold sea currents. A marsh is defined as a "characteristic ecosystem of the highest part of the coastal low-lying platforms, occupying the space between the low water neaps and the high water springs. Morphologically it corresponds to the high *slike* and *schorre*; it is, therefore, an amphibious ecosystem, with muddy or silty soils, salty, colonized by halo-helophytic herbaceous vegetation. It develops in estuaries, deltas, lagoons and marine swamplands, especially in extratropical regions" (Moreira, 1984, p. 109).

In the intertropical zone of the African continent, mangrove ecosystems are found mainly on the eastern coasts influenced by warm sea currents, as in Mozambique, for instance (Beentje & Bandeira, 2007) where the coastline is influenced by the Mozambique Warm Current, which extends southwards by the Agulhas Current. Mangroves are also common along the coasts of West Africa, from Senegal to Angola (Ward *et al.*, 2016).

Although at a similar latitude to Mozambique, Angola's coastline is influenced by the Benguela Cold Current and, therefore, the low-energy environments at the mouths of the major watercourses and sheltered inlets are dominated by marshes, although mangroves also occur. However, mangroves on the western coasts of the continents, apart from being less frequent, have a much lower floristic richness than those on the eastern coasts (Moreira, 1977). In Angola, mangroves have shown a very significant decrease due to anthropic action (cutting trees for wood, systematic felling of all vegetation to eradicate diseases, land conversion for agriculture and pollution, among others). In the past, they extended south to Lobito where they are now extinct. Mangroves do not occur in the south of Lobito and along the coast of southwest Angola and Namibia, and the amphibian vegetation of muddy or sandy tidal platforms consists exclusively of saltmarshes.

The occurrence of saltmarshes in the west African coast north of the Cape of Boa Esperança is associated with the Benguela Cold Current, which constitutes a wide flow towards northwest forming the eastern branch of the South Atlantic circulation cell. Typically, cold water from the South Atlantic circulation flows up the west coast of Africa to the latitude of Benguela, about 16° South. The upwelling system known as the Benguela Upwelling System consists of a rise in cold, nutrient-rich water from depths of around 200-300m, which is responsible for the high productivity of Angola's southwest ecosystems (Kirkman & Nsingi, 2019). However, its influence is irregular as to water characteristics, temperature, northern latitude reach, current intensity, etc. These oscillations are related to two phenomena: on the one hand, frequently warm and nutrient-poor waters from the South Indian Ocean Current, called the Agulhas Current, mix with the Benguela Current, making the thermal (and other) characteristics of the latter chaotic (Veitch & Peven, 2017); on the other hand, about once every 10 years (Mann & Lazier, 2006), during the process known as the Benguela Niño Current (Imbol Koungue *et al.*, 2019), the Angolan Warm Current extends abnormally southwards from the usual 15° S up to 25° S, extending also offshore up to 150km and with a depth of 50m (Richter *et al.*, 2010).

Due to the double influence of the Angolan Hot Current and the Benguela Cold Current on the Angolan coast, we find that all mangroves are located north of Lobito, and, in this entire sector, marshlands are floristically reduced to few succulent species (in most cases only *Sarcocornia natalensis* subsp. *affinis* (Moss) S.Steffen, Mucina & G.Kadereit), which are characteristic of marshlands of the inland sector of the mangrove forest, in contact with continental ecosystems. These very impoverished versions of marshes had also been identified for the coast of Mozambique in the inland mangrove sector (Moreira, 1977). In these versions, which Moreira (1977) calls "salty swamps", are present species as *Sesuvium portulacastrum* (L.) L. and *Sporobolus virginicus* (L.) Kunth, among others, which also occur in Angolan marshlands. No mangroves occur south of Lobito, a reality that extends through all the Namibian territory, as in both the southwest of Angola and in the Namibian coast, the tide-influenced muddy or sandy-muddy platforms, where in low energy environments, are colonised by marsh vegetation. Globally, in terms of floristic richness, these marshlands are frankly poorer than the Western Europe ones (and poorer than all the Holarctic Kingdom saltmarshes) of both Mediterranean and temperate oceanic climates (Cardoso, 2014; Costa *et al.*, 2009). This area is characterized by a desert to semi-desert climate, where fresh water supplies are extremely scarce, unlike in the European marshes, especially those in the Eurosiberian Region. In Angola the saltmarshes have their northernmost position in the Cuanza River estuary (near Luanda), where a very impoverished version of these communities occupies a narrow strip in the most inland sector of the mangrove forest, which occures extensively along this river.

The study we are presenting is the first phytosociological analysis of the saltmarshes and brackish marshes of the southwest of Angola and, as such, the communities identified are unprecedented for science. We also make a description of the environmental characteristics in which each community is included, as well as their floristic separation mainly through indicator species.

II. MATERIAL AND METHODS

The vegetation relevés were collected according to the sigmatist and dynamic-catenal phytosociology approach (Braun-Blanquet, 1979; Géhu & Rivas-Martínez, 1981; Rivas-Martínez, 1976, 2005; Theurillat *et al.*, 2020). A floristic-statistical group analysis (Müller-Dombois & Ellenberg, 1974) was used for community definitions and synthetic table arrangements. The bioclimatic typology was based on the work of Rivas-Martínez *et al.* (2011). For the identification of collected specimens, the most relevant bibliography for the area was used, namely Flora Zambesiaca, Flora of Tropical Africa, Flora of Southern Africa, Flora of Tropical East Africa, Conspectus Florae Angolensis (Brummitt, 1992; Exell & Fernandes, 1961; Exell *et al.*, 1970; Exell & Mendonça, 1937, 1951, 1954; Klaassen & Craven, 2003; Ornold & De Wet, 1993; Retief & Herman, 1997; Vollesen, 2000) and their comparison with duly identified herbarium specimens (LISC herbarium, University of Lisbon). The nomenclature used follows the *Plants of the World Online* database (Plants of the World Online [POWO], 2019).

The Braun-Blanquet scale values were converted to numerical values based on the Müller-Dombois and Ellenberg methodology (1974), and a Principal Component Analysis (PCA) was applied to the matrix containing all the relevés using the *Canoco 5.5 software* (Ter Braak & Šmilauer, 2012).

III. CHARACTERIZATION OF THE REGION

This work was carried out in the coastal saltmarshes and brackish areas of the Namibe Province. This territory comprises the coastal strip of the Namib Desert and is crossed by the Bero and the Pindo rivers with water almost all year round. The Bero estuary is next to the city of Namibe (formerly known as Moçâmedes) and the Pindo estuary near Tombua (formerly known as Porto Alexandre). Occurring in a desert area (mostly a sandy desert), the Angolan saltmarshes in the studied region belong to the silt-loam textural class or even the sandy-loam class (Cardoso *et al.*, 2019).

This area is characterized by a tropical hyperdesert, upper thermotropical, lower hyperarid, attenuated hyper-oceanic bioclimate (fig. 1) (Cardoso, 2014; Rivas-Martínez *et al.*, 2011).

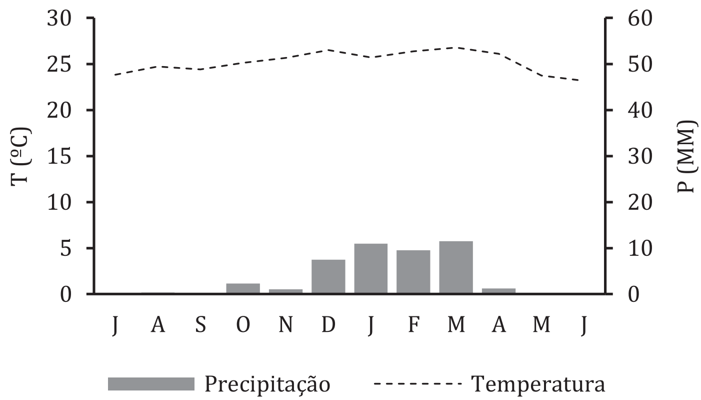

Fig. 1 – Thermopluviometric diagram for Namibe city (Namibe Weather Station – ID 857 331, Lat. 15 159; Long. 12 178; Alt. 11m; Hyperdesertic tropical, superior thermotropical, inferior hyperarid, attenuated hyperoceanic), 2014-2020.

Fig. 1 – Diagrama termopluviométrico da cidade do Namibe (Estação Meteorológica do Namibe – ID 857331, Lat. 15 159; Long. 12 178; Alt. 11m; Tropical hiperdesértico, termotropical superior, hiperárido inferior, hiperoceânico atenuado), 2014-2020.

Source: Southern African Science Centre for Climate Change and Adaptative Land Management [SASSCAL] WeatherNet (2020)

IV. RESULTS AND DISCUSSION

1. New associations

The occurrence of 18 species, belonging to eight families (Appendix 1) and six new associations were reported for the saltmarshes and brackish marshes along the coast of the southwest of Angola, which we now describe:

1. ***Sarcocornietum affinis*** J.F. Cardoso, J.C. Costa, Neto, Maria C. Duarte & Monteiro--Henriques *ass. nov.*
(table I, *holotypus* relevé no. 7)

Halophilous chamaephytic association of *Sarcocornia natalensis* subsp. *affinis*, often monospecific, although sometimes *Sporobolus virginicus* and *Sesuvium portulacastrum,* may also occur in its floristic composition.

The bioclimate of the areas where it occurs varies from tropical xeric to tropical hyperdesert. We place this community in the *Arthrocnemetea franzii* class (coastal salt-water marshes flooded by sea tides or occasionally interior saline waters: succulent shrub, forbs and grass communities, growing in infra-thermotropical desertic and xeric bioclimate of tropical west coast of Africa), order *Sarcocornio-Salicornietalia meyerianae* (halophytic vegetation of small succulent plants); *Sarcocornion decumbentis* alliance (flooded communities; Boucher & Jarman, 1977; Hanekom *et al.*, 2009; Mucina *et al.*, 2003; Rivas--Martínez *et al.*, 2017).

Sarcocornia natalensis subsp. *affinis* was first reported for Angola by Cardoso (2014) as part of the fieldwork conducted during this study. This species was listed in *Plantas de Angola* (Figueiredo & Smith, 2008) as *Arthrocnemum macrostachyum* (currently *Arthrocaulon macrostachyum*). However, the genus *Arthrocnemum* has one undivided cavity in the axis after the detachment of the flowers while the specimens we observed, in the Namibe saltmarshes, have three cavities which correspond to the genus *Sarcocornia* (*S. natalensis* subsp. *affinis*). It is a prostrate, rhizomatous chamaephyte, woody at the base, succulent, with segments of 5-15mm long and 2-3mm in diameter, corresponding to the description made by Le Roux and Wahl (2005).

Table I – Phytosociological table of the association Sarcocornietum affinis.

Quadro I – Quadro fitossociológico da associação Sarcocornietum affinis.

Area (m^2)	1	**1**	1	1	4	2	2	2	2	4	2	4	4	1	2	4	
No. of taxa	1	**1**	1	1	2	2	2	2	2	3	2	4	3	2	2	2	
Relevé no.	6	**7**	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
Characteristics																	
Sarcocornia natalensis subsp. *affinis*	5	**5**	5	4	3	4	4	3	5	4	3	2	3	5	5	4	V
Sporobolus virginicus	.	**.**	.	.	.	.	.	.	.	2	1	2	1	+	1	3	II
Sesuvium portulacastrum	.	**.**	.	.	.	3	1	2	1	2	.	.	.	.	.	.	II
Cyperus laevigatus	.	**.**	.	.	.	.	.	.	.	.	.	.	3	.	.	.	+
Suaeda merxmuelleri	.	**.**	.	.	.	.	.	.	.	.	.	1	.	.	.	.	+
Companions																	
Chloris flabellata	.	**.**	.	.	1	.	.	.	.	.	.	.	.	.	.	.	+
Eragrostis prolifera	.	**.**	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+
Mesembryanthemum dimorphum	.	**.**	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+

Places: 6, 15, 16 Bero river (Namibe); 7, 11, 12, 13, 17 Pindo river (Tombua); 8, 14, 20, 21 Lobito; 9, 10 Cubai (Sumbe); 18, 19 Salinas Sol (Namibe).

2. ***Suaedetum merxmuelleri*** J.F. Cardoso, J.C. Costa, Neto, Maria C. Duarte & Monteiro-Henriques *ass. nov.*
(table II, *holotypus* relevé no. 52)

This plant community, with a distribution in tropical desertic and hyperdesertic, upper thermotropical, ultrahyperarid to hyperarid, attenuated hyperoceanic (semi-hyperoceanic) bioclimate, is characterized, almost exclusively, by *Suaeda merxmuelleri,* an endemic nanophanerophyte (bush) of the southwest of Angola, sometimes accompanied by *Sporobolus virginicus, Sesuvium portulacastrum* and *Juncus rigidus*. It is found in the highest areas of the saltmarsh, with a brackish water table, and it is only occasionally flooded, sometimes by brackish waters after heavy rains. Being a desert with tropical characteristics, the soil is subjected to strong salinization for most of the year. Salinity oscillations can be high although low values can be recorded very sporadically during the scarce rainy periods. It is a frequent association in nitrified sites (with anthropic disturbance) along roads and paths. Very common in the studied area, also occurring further in the north, in Lobito marshes. We have placed this community in *Arthrocnemetea franzii*, *Sarcocornio-Juncetalia kraussii* (halophilous nanophanerophytic vegetation), *Spergulario mediae-Puccinellion angustae* (dense communities rich in Amaranthaceae and halotolerant grasses, adapted to brackish water flooding) (Boucher & Jarman, 1977; Hanekom *et al.*, 2009; Mucina *et al.*, 2003; Rivas-Martínez *et al.*, 2017).

Table II – Phytosociological table of the association Suaedetum merxmuelleri.

Quadro II – Quadro fitossociológico da associação Suaedetum merxmuelleri.

Area (m^2)	**1**	1	1	1	2	2	4	4	8	4	4	8	8	4	
No. of taxa	**1**	1	1	1	1	2	2	2	5	2	2	3	3	2	
Relevé no.	**52**	53	54	55	56	57	58	59	60	61	62	63	64	65	
Characteristics															
Suaeda merxmuelleri	**5**	5	5	4	4	3	4	3	3	5	5	4	3	4	V
Sporobolus virginicus	.	.	.	.	.	.	+	1	3	+	2	2	2	.	III
Sesuvium portulacastrum	.	.	.	.	.	.	.	.	.	.	.	.	.	2	+
Juncus rigidus	.	.	.	.	.	.	.	.	1	.	.	.	.	.	+
Cressa salina	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+
Companions															
Phragmites mauritianus	.	.	.	.	.	.	.	.	.	.	.	.	4	.	+
Mesembryanthemum pseudoschlichtianum	.	.	.	.	.	1	.	.	.	.	.	.	.	.	+
Chloris flabellata	.	.	.	.	.	.	.	.	.	.	.	1	.	.	+
Felicia mossamedensis	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+
Mesembryanthemum dimorphum	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+

Places: 52, 55, 65 Bero river (Namibe); 53, 63 Namibe; 54, 61 Lobito; 56, 57, 58, 59, 60, Pindo river (Tombua); 62, 64 Salinas Sol (Namibe).

3. ***Cypero laevigati-Cressetum salinae*** J.F. Cardoso, J.C. Costa, Neto, Maria C. Duarte & Monteiro-Henriques *ass. nov.*
(table III, *holotypus* relevé no. 3)

This community is dominated by halophilous annual (therophytes) and stoloniferous (hemicryptophytes) species, with fugacious hydromorphy (only when heavy rainfall occurs), inserted in a tropical hyperdesert, upper thermotropical, lower ultrahyperarid, attenuated hyperoceanic (semi-hyperoceanic) bioclimate. It is characterized by *Cressa salina*, *Sporobolus virginicus* and *Cyperus laevigatus*. This community is infrequent, having been observed only in moderately nitrified saline habitats with short flood periods, near the city of Namibe. We consider it to be a geovicarious of the *Cressetum salinae* association, present in Cabo Verde, where it also occurs in temporarily flooded sandy soils (Rivas-Martínez *et al.*, 2017). This association has been positioned in the *Arthrocnemetea franzii* class, *Sarcocornio-Juncetalia kraussii* order, *Spergulario mediae-Puccinellion angustae* alliance.

Table III – Phytosociological table of the association Cypero laevigati-Cressetum salinae.

Quadro III – Quadro fitossociológico da associação Cypero laevigati-Cressetum salinae.

Area (m^2)	1	1	**4**	2	4
No. of taxa	1	1	**2**	2	2
Relevé no.	1	2	**3**	4	5
Characteristics					
Cressa salina	4	5	**5**	4	3
Sporobolus virginicus	.	.	**.**	1	2
Cyperus laevigatus	.	.	+	.	.
Places: 1, 3 Namibe; 2, 4, 5 Salinas Sol (Namibe)					

4. ***Junco rigidi-Sporoboletum virginici*** J.F. Cardoso, J.C. Costa, Neto, Maria C. Duarte & Monteiro-Henriques *ass. nov.*
(table IV, *holotypus* relevé no. 48)

This community was observed in occasionally flooded depressions, in solonchak arenic soils with very occasional hydromorphy (characterized by a strong concentration of soluble salts due to strong evaporation, in desert and semi-desert climates). It is composed almost exclusively by *Sporobolus virginicus*, sometimes accompanied by *Juncus rigidus*, and, in the higher areas, by *Suaeda merxmuelleri*. In areas where the flooding period is longer, the lower salinity allows the occurrence of reed (*Phragmites mauritianus*). Besides the study area, we also observed this community further north, at Lobito. This community occurs in tropical hyperdesert, upper thermotropical, ultrahyperarid to hyperarid, hyperoceanic attenuated (semi-hyperoceanic) bioclimate, although it can occur in tropical desert and xeric bioclimate too. It has been placed in the *Arthrocnemetea franzii* class, *Sarcocornio-Juncetalia kraussii* order and *Spergulario mediae-Puccinellion angustae* alliance.

Table IV – Phytosociological table of the association Junco rigidi-Sporoboletum virginici.

Quadro IV – Quadro fitossociológico da associação Junco rigidi-Sporoboletum virginici.

Area (m^2)	1	1	1	1	1	1	4	2	4	**4**	4	8	4	
No. of taxa	1	1	1	1	1	2	2	2	2	**2**	3	3	2	
Relevé no.	39	40	41	42	43	44	45	46	47	**48**	49	50	51	
Characteristic														
Sporobolus virginicus	5	5	5	5	4	4	2	3	4	**4**	4	4	4	V
Juncus rigidus	.	.	.	.	.	.	.	.	.	+	1	.	.	I
Suaeda merxmuelleri	.	.	.	.	.	.	.	.	.	**.**	+	1	.	I
Cressa salina	.	.	.	.	.	.	.	.	.	**.**	.	.	2	+
Companions														
Phragmites mauritianus	.	.	.	.	.	.	.	.	3	**.**	.	2	.	I
Brachiaria psammophila	.	.	.	.	.	.	3	.	.	**.**	.	.	.	+
Stipagrostis prodigiosa	.	.	.	.	.	+	.	.	.	**.**	.	.	.	+
Mesembryanthemum pseudoschlichtianum	.	.	.	.	.	.	.	+	.	**.**	.	.	.	+
Places: 39 Namibe; 40, 50, 51 Salinas Sol (Namibe); 41, 43, 44, 45, 46, 47, 48, 49 Pindo (Tombua); 42 Lobito.														

5. ***Sesuvietum crithmoidis*** J.F. Cardoso, J.C. Costa, Neto, Maria C. Duarte & Monteiro-Henriques *ass. nov.*
(table V, *holotypus* relevé no. 23)

Halonitrophilous, psammophilous and monospecific community of the perennial *Sesuvium crithmoides* (= *S. mesembryanthemoides*, = *S. crystallinum*) sometimes accompanied by *Zygophyllum simplex* (table V). It occurs on intertidal sands, flooded by oceanic waters usually at maximum tidal level, where the sea deposits organic (responsible for the nitrification) and inorganic debris. The relevés were collected in areas characterized by tropical hyperdesertic and desertic, thermotropical, ultrahyperarid to arid, hyperoceanic attenuated (semi-hyperoceanic) bioclimate. According to our observations, this community occurs along the maritime dunes at least up to Luanda (tropical xeric bioclimate).

The taxon *Sesuvium crithmoides*, previously considered endemic in Angola, was recently (Sukhorukov *et al.*, 2018) observed on the sandy coast of the Democratic Republic of Congo.

We have placed this association in the *Arthrocnemetea franzii* class, *Sesuvietalia persoonii* order (communities of succulent stolonate, hydro-halophytic and aero-halophytic species from the western coasts of Africa, from Morocco to South Africa, in infra-thermotropical, ultrahyperarid to arid bioclimate) and *Sesuvion persoonii* alliance (see Costa, 2018; Rivas-Martínez *et al.*, 2017).

Table V – Phytosociological table of the association Sesuvietum crithmoidis.
Quadro V – Quadro fitossociológico da associação Sesuvietum crithmoidis.

Area (m^2)	10	**10**	10	10	10	10	10	10	
No. of taxa	1	**1**	1	1	2	2	2	2	
Relevé no.	22	**23**	24	25	26	27	28	29	
Characteristic									
Sesuvium crithmoides	4	**4**	2	3	3	3	2	2	V
Companions									
Zygophyllum simplex	.	**.**	.	.	+	1	1	.	II
Brachiaria psammophila	.	**.**	.	.	.	.	.	1	I

Places: 22 Namibe foz do rio Bero; 23, 26, 27, 28 Praia Sacomar (Namibe); 24, 25, 29 Praia Amélia (Namibe)

6. ***Sarcocornio affinis-Sesuvietum portulacastri*** J.F. Cardoso, J.C. Costa, Neto, Maria C. Duarte & Monteiro-Henriques *ass. nov.*
(table VI, *holotypus* relevé no. 37)

Halophilous community dominated by *Sesuvium portulacastrum*, a perennial, succulent, pioneer species, of pantropical distribution, accompanied by *Sarcocornia natalensis* subsp. *affinis*, typical of saltmarshes and sandy depressions flooded and submerged by brackish waters for more or less long periods. It occurs in tropical hyperdesertic and desertic, thermotropical, ultrahyperarid to hyperarid, hyperoceanic attenuated (semi-

-hyperoceanic) bioclimate. According to our observations it occurs in Lobito marshes and southward until the river Cunene estuary, almost always in monospecific formations. It is a geovicarious of the Cape Verde association *Sesuvietum portulacastri*, also dominated by *Sesuvium portulacastrum* (Rivas-Martínez *et al.*, 2017), however, in SW Angola this species is accompanied by *Sarcocornia natalensis* subsp. *affinis* and *Sporobolus virginicus*, which do not occur in Cape Verde. We also include this community in the *Sesuvietalia persoonii* order and *Sesuvion persoonii* alliance.

Table VI – Phytosociological table of the association Sarcocornio affinis-Sesuvietum portulacastri.

Quadro VI – Quadro fitossociológico da associação Sarcocornio affinis-Sesuvietum portulacastri.

Area (m^2)	1	2	1	1	1	1	1	**1**	4	
No. of taxa	1	1	1	1	1	2	2	**2**	3	
Relevé no.	30	31	32	33	34	35	36	**37**	38	
Characteristic										
Sesuvium portulacastrum	5	5	5	4	4	4	4	**5**	3	V
Sarcocornia natalensis subsp. *affinis*	.	.	.	.	2	2	3	**1**	2	III
Sporobolus virginicus	.	.	.	.	.	.	.	**.**	1	+
Places: 30, 31, 35, 35 rio Bero (Namibe); 32, 36, 37 rio Pindo (Tombua); 33, 38 Lobito.										

2. Multivariate analysis (ordination) of the relevés

The relevés were collected in a table and the Braun-Blanquet scale values were converted into numerical values to be used in a Principal Component Analysis (PCA). The purpose of this analysis was primarily to determine the dispersion patterns of the relevés as a result of their floristic composition. The closest points correspond to similar relevés in terms of floristic composition and the farthest points correspond to more dissimilar relevés. In this way we can test the manual organisation of the relevés that has been carried out with the previously presented tables and the respective plant associations. The observed structure, although being the result of the floristic composition of the relevés, is also the result of the implicit effect of the environmental factors, which were discussed in the description of each of the plant communities.

Figures 2 and 3, resulting from the PCA, show a good segregation of the plant communities described (fig. 2) and clearly characterized by the bioindicator species presented (fig. 3). *Suaeda merxmuelleri* is the diagnostic species of the association *Suaedetum merxmuelleri*; *Sporobolus virginicus* is the diagnostic species of the association *Junco rigidi-Sporoboletum virginici*; *Sarcocornia affinis* is the diagnostic species of the association *Sarcocornietum affinis*; *Sesuvium portulacastrum* is the diagnostic species of the association *Sarcocornio affinis-Sesuvietum portulacastri*; *Cressa salina* is the diagnostic species of the association *Cypero laevigati-Cressetum salinae*; and *Sesuvium crithmoides* is the diagnostic species of the association *Sesuvietum crithmoidis*.

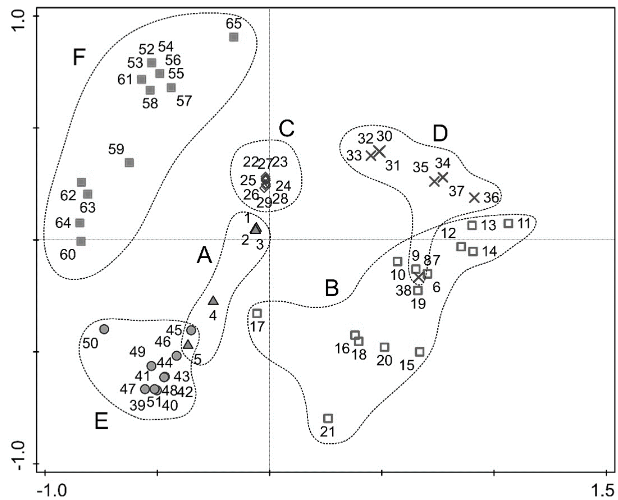

Fig. 2 – Principal Component Analysis (PCA) – plot showing the ordination of vegetation samples.

Fig. 2 – Análise de Componentes Principais (ACP) – plot com a ordenação de amostras de vegetação.

A. Cypero laevigati-Cressetum salinae (*samples* 1-5); **B.** Sarcocornietum affinis (*samples* 6-21); **C.** Sesuvietum crithmoidis (*samples* 22-29); **D.** Sarcocornio affinis-Sesuvietum portulacastri (*samples* 30-38); **E.** Junco rigidi-Sporoboletum virginici (*samples* 39-51); **F.** Suaedetum merxmuelleri (*samples* 52-65).

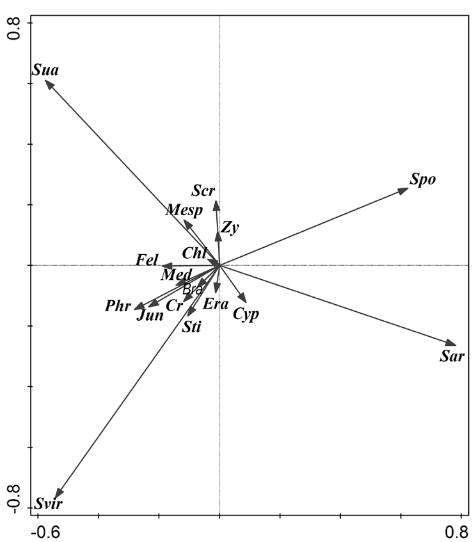

Fig. 3 – Principal Component Analysis – plot showing the ordination of species.

Fig. 3 – Análise de Componentes Principais – plot com a ordenação das espécies.

Chl (Chloris flabellata); **Cr** (Cressa salina); **Cyp** (Cyperus laevigatus); **Era.** (Eragrostis prolifera); **Fel** (Felicia mossamedensis); **Jun** (Juncus rigidus); **Bra** (Brachiaria psammophila); **Phr** (Phragmites mauritianus); **Med** (Mesembryanthemum dimorphum); **Mesp** (Mesembryanthemum pseudoschlichtianum); **Sar** (Sarcocornia natalensis *subsp*. affinis); **Scr** (Sesuvium crithmoides); **Spo** (Sesuvium portulacastrum); **Svir** (Sporobolus virginicus); **Sti** (Stipagrostis prodigiosa); **Sua** (Suaeda merxmuelleri); **Zy** (Zygophyllum simplex).

Syntaxonomical scheme (in bold, new *syntaxa* described in the context of this work):

Class: Arthrocnemetea franzii Rivas-Martínez, Lousã, J.C. Costa & Maria C. Duarte 2017

Order: Sesuvietalia persoonii Rivas-Martínez, Lousã, J.C. Costa & Maria C. Duarte 2017 *corr.* Rivas-Martínez, Lousã, J.C. Costa & Maria C. Duarte in J.C. Costa 2018

Alliance: Sesuvion persoonii Lousã, J.C. Costa & Maria C. Duarte 2017 *corr.* Rivas-Martínez, Lousã, J.C. Costa & Maria C. Duarte in J.C. Costa 2018

Sesuvietum crithmoidis J.F. Cardoso, J.C. Costa, Neto, Maria C. Duarte & Monteiro-Henriques (new)

Sarcocornio affinis-Sesuvietum portulacastri J.F. Cardoso, J.C. Costa, Neto, Maria C. Duarte & Monteiro-Henriques (new)

Order: Sarcocornio-Salicornietalia meyerianae Boucher ined.

Alliance: Sarcocornion decumbentis Mucina, Jansen & O' Callaghaen 2003

Sarcocornietum affinis J.F. Cardoso, J.C. Costa, Neto, Maria C. Duarte & Monteiro-Henriques (new)

Order: Sarcocornio–Juncetalia kraussii Boucher ined.

Alliance: Spergulario mediae-Puccinellion angustae Mucina, Jansen & O'Callaghan 2003

Suaedetum merxmuelleri J.F. Cardoso, J.C. Costa, Neto, Maria C. Duarte & Monteiro-Henriques (new)

Cypero laevigati-Cressetum salinae J.F. Cardoso, J.C. Costa, Neto, Maria C. Duarte & Monteiro--Henriques (new)

Junco rigidi-Sporoboletum virginici J.F. Cardoso, J.C. Costa, Neto, Maria C. Duarte & Monteiro--Henriques (new)

V. CONCLUSIONS

The coastal region of the southwest of Angola (south of Lobito), despite being under a tropical macrobioclimate, presents no mangroves in its coastal swamps. Instead, saltmarshes are present, much probably owing to the influence of the cold oceanic waters of the Benguela Cold Current. These marshes are floristically very poor and often monospecific. This is a substantially different situation from the South African and Holarctic marshes characterized by a much greater floristic richness. Angolan marshlands are characterized by a dominance of fine sandy soil texture which is associated to the presence of the extensive field of dunes typical of the Namib Desert. The research carried out during 2010-2015 and 2018 allowed to analyse the floristic composition of the Namibe province's marshlands, as well as the originality of the floristic combinations associated to the more or less differentiated environments.

In this way, a total of six new plant associations were described. Their spatial distribution is related to the ecological gradients associated to water table salinity, time of submersion by sea waters, soil texture, as well as nitrogen levels. These communities, clearly segregated by the PCA, do not present a seral logic and, therefore, as a whole, constitute an original geopermasigmetum, presented for the first time in this work.

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REFERENCES

Beentje, H., & Bandeira, S. (2007). *Field Guide to the Mangrove Trees of Africa and Madagascar*. Kew Publishing.

Boucher, C., & Jarman, M. L. (1977). The vegetation of the Langebaan area, South Africa. *Transaction of the Royal Society of South Africa*, *42*(3-4), 241-272. https://doi.org/10.1080/00359197709519916

Braun-Blanquet, J. (1979). *Fitosociología: bases para el estudio de las comunidades vegetales* [Phytosociology: bases for the study of plant communities]. Blume.

Brummitt, R. K. (1992). *Vascular plant families and genera*. Royal Botanic Gardens.

Cardoso, J. (2014). *Estudo Geobotânico do Sudoeste angolano desde a Tundavala ao Tombua* [Geobotanical study of Southwest Angola from Tundavala to Tombua]. Universidade de Lisboa.

Cardoso, J., Fonseca, J. P., Aguiar, C., Bioret, F., Neto, C., & Costa, J. C. (2019). Contribuição para o conhecimento das comunidades vegetais de *Welwitshschia mirabilis* (Welwitschiaceae, Gnetophyta) do deserto do Namibe, Angola [Contribution to the knowledge of the *Welwitshschia mirabilis* (Welwitschiaceae, Gnetophyta) plant communities in the Namibe desert, Angola]. *International Journal in Portuguese Language*, *4*(35), 133-149. https://doi.org/10.31492/2184-2043.RILP2018.35/pp.133-149

Costa, J. C. (2018). *Sesuvium* syntaxa nomenclatura correction of Cabo Verde islands. *International Journal of Geobotanical Research*, *8*(1), 25-25.

Costa, J. C., Arsénio, P., Monteiro, T., Neto, C., Pereira, E., Almeida, T., & Izco, J. (2009). Finding the boundary betwen Eurosiberian and Mediterranean Salt Marshes. *Journal of Coastal Research*, *56*(2), 1340-1344.

Exell, A. W., & Fernandes, A. (1961). Crassulaceae. In A. Fernandes, & E. J. Mendes (Eds.), *Conspectus Florae Angolensis* (pp. 5-39). Instituto de Investigação Científica Tropical.

Exell, A. W., & Mendonça, F. A. (1937). Ranunculaceae-Aquifoliaceae. In L. W. Carriço (Ed.), *Conspectus Florae Angolensis* (pp. 1-176). Instituto Botânico de Coimbra/Museu Britânico.

Exell, A. W., & Mendonça, F. A. (1951). Malvaceae-Aquifoliaceae. In L. W. Carriço (Ed.), *Conspectus Florae Angolensis* (pp. 177-422). Junta de Investigações do Ultramar, Instituto de Investigação Científica de Angola.

Exell, A. W., & Mendonça, F. A. (1954). Celastraceae-Connaraceae. In Junta de Investigações do Ultramar (Ed.), *Conspectus Florae Angolensis* (pp. 1-152). Junta de Investigações do Ultramar, Instituto de Investigação Científica de Angola.

Exell, A. W., Fernandes, A., & Mendes, E. J. (1970). Rosaceae-Alangiaceae. In *Conspectus Florae Angolensis* (pp. 1-401). Junta de Investigações do Ultramar, Instituto de Investigação Científica de Angola.

Figueiredo, E., & Smith, G. F. (2008). *Plantas de Angola. Strelitzia* 22 [Plants of Angola. Strelitzia 22]. South African National Botanical Institute.

Géhu, J.-M., & Rivas-Martínez, S. (1981). Notions fondamentales de phytosociologie [Fundamentals of phytosociology]. In H. Dierschke (Ed.), *Syntaxonomie* [Syntaxonomy] (pp. 5-33). J. Cramer.

Hanekom, N., Randall, R. M., Nel, P., & Kruger, N. (2009). *West Coast National Park – State of Knowledge*. South African National Parks.

Imbol Koungue, R. A., Rouault, M., Illig, S., Brandt, P., & Jouanno, J. (2019). Benguela Niños and Benguela Niñas in Forced Ocean Simulation From 1958 to 2015. *Journal of Geophysical Research: Oceans*, *124*(8), 5923-5951. https://doi.org/10.1029/2019JC015013

Kirkman, S. P., & Nsingi, K. K. (2019). Marine Biodiversity of Angola: Biogeography and Conservation. In B. Huntley, V. Russo, F. Lages, & N. Ferrand (Eds.), *Biodiversity of Angola* (pp. 43-52). Springer. https://doi.org/10.1007/978-3-030-03083-4_3

Klaassen, E. S., & Craven, P. (2003). *Checklist of grasses in Namibia. Southern African Botanical Diversity Network Report No. 20*. SABONET.

Le Roux, A., & Wahl, Z. (2005). *Namaqualand. South African Wild Flower Guide 1* (3rd Ed.). Botanical Society of South Africa.

Mann, K. H., & Lazier, J. R. (2006). *Dynamics of Marine Ecosystems: Biological-Physical Interactions in the Oceans*. Blackwell Publishing.

Moreira, E. (1977). Nota sobre o ecossistema de mangal no Sul de Moçambique [Note on the mangrove ecosystem in southern Mozambique]. *Garcia de Orta – Série de Geografia*, *4*(1-2), 29-44.

Moreira, E. (1984). *Glossário de termos usados em Geomorfologia Litoral* [Glossary of used terms in Coastal Geomorphology]. Centro de Estudos Geográficos.

Mucina, L., Jansen, J., & O' Callaghaen, M. (2003). Syntaxonomy and zonation patterns in coastal salt marshes of the Uilkraals Estuary. *Phytocoenologia*, *32*(2-3), 309-334. https://doi.org/10.1127/0340-269X/2003/0033-0309

Müller-Dombois, D., & Ellenberg, H. (1974). *Aims and methods of vegetation ecology*. John & Wiley & Sons.

Ornold, T. H., & De Wet, B. C. (1993). *Plants of Southern Africa: names and distribution*. National Botanical Institute.

Plants of the World Online. (2019). *Plants of the World Online*. Plants of the World Online, Royal Botanic Gardens. http://www.plantsoftheworldonline.org/

Retief, E., & Herman P. P. J. (1997). *Plants of the Northern Provinces of South Africa: Key and diagnostic characters*. National Botanical Institute.

Richter, I., Behera, S. K., Masumoto, Y., Taguchi, B., Komori, N., & Yamagata, T. (2010). On the triggering of Benguela Niños: Remote equatorial versus local influences. *Geophysical Research Letters*, *37*(20). https://doi.org/10.1029/2010GL044461

Rivas-Martínez, S. (1976). Sinfitosociología, una nueva metodología para el estudio del paisaje vegetal [Symphitosociology, a new methodology for the study of the vegetal landscape]. *Anales del Instituto Botánico A. J. Ca-vanilles*, *33*, 179-188.

Rivas-Martínez, S. (2005). Notions on dynamic-catenal phytosociology as a basis of landscape science. *Plant Biosystems*, *139*(2), 135-144. https://doi.org/10.1080/11263500500193790

Rivas-Martínez, S., Lousã, M., Costa, J. C., & Duarte, M. C. (2017). Geobotanical survey of Cabo Verde Islands (West Africa). *International Journal of Geobotanical Research*, *7*, 1-103. https://doi.org/10.5616/ijgr170001

Rivas-Martínez, S., Rivas Sáenz, S., & Penas, A. (2011). Worldwide Bioclimatic Classification System. *Global Geobotany*, *1*, 1-63.

Southern African Science Centre for Climate Change and Adaptative Land Management WeatherNet. (2020). *SASSCAL WeatherNet*. SASSCAL WeatherNet. www.sasscalweathernet.org

Sukhorukov, A., Nilova, M., Erst, A., Kushunina, M., Baider, C., Verloove, F., Salas-Pascual, M., Belyaeva, I. V., Krinitsina, A. A., Bruyns, P. V., & Klak, C. (2018). Diagnostics, taxonomy, nomenclature and distribution of perennial Sesuvium (Aizoaceae) in Africa. *PhytoKeys*, *92*, 45-88. https://doi.org/10.3897/phytokeys.92.22205

Ter Braak, C. J., & Šmilauer, P. (2012). *Canoco Reference Manual and User's Guide: Software for Ordination, Version 5.0*. Microcomputer Power.

Theurillat, J. P., Willner, W., Fernández-González, F., Bültmann, H., Čarni, A., Gigante, D., Mucina, L., & Weber, H. (2020). International Code of Phytosociological Nomenclature, 4th edition. *Applied Vegetation Science. Conservation, restoration and survey of plant communities, 24*(1), e12491. https://doi.org/10.1111/avsc.12491

Veitch, J. A., & Penven, P. (2017). The role of the Agulhas in the Benguela Current system: A numerical modelling approach. *Journal of Geophysical Research: Oceans*, *122*(4), 3375-3393. https://doi.org/10.1002/2016JC012247

Vollesen, K. (2000). *Blepharis (Acanthaceae) A Taxonomic Revision*. The Board of Trustees of the Royal Botanic Gardens.

Ward, R. D., Friess, D. A., Day, R. H., & MacKenzie, R. A. (2016). Impacts of climate change on mangrove ecosystems: a region by region overview. *Ecosystem Health and Sustainability, 2*(4), ee01211. https://doi.org/10.1002/ehs2.1211

APPENDIX 1. LIST OF PRESENTED TAXA

Arthrocnemum macrostachyum (Moric.) K.Koch = Arthrocaulon macrostachyum (Moric.) Piirainen & G.Kadereit (Amaranthaceae)
Brachiaria psammophila (Welw. ex Rendle) Launert (Poaceae)
Chloris flabellata (Hack.) Launert (Poaceae)
Cressa salina (J.A. Schmidt) Rivas Mart., Lousã, J.C.Costa & Maria C. Duarte (Convolvulaceae)
Cyperus laevigatus L. (Cyperaceae)
Eragrostis prolifera (Sw.) Steud. (Poaceae)
Felicia mossamedensis (Hiern) Mendonça (Asteraceae)
Juncus rigidus Desf. (Juncaceae)
Mesembryanthemum dimorphum Welw. ex Oliv. [=*Psilocaulon dimorphum* (Welw. ex Oliv.) N.E.Br.] (Aizoaceae)
Mesembryanthemum pseudoschlichtianum (S.M.Pierce & Gerbaulet) Klak (=*Brownanthus pseudoschlichtianus* S.M.Pierce & Gerbaulet) (Aizoaceae)
Phragmites mauritianus Kunth (Poaceae)
Sarcocornia natalensis subsp. *affinis* (Moss) S.Steffen, Mucina & G.Kadereit
Sesuvium crithmoides Welw. (= *S. mesembryanthemoides* Wawra = *S. crystallinum* Welw. ex Oliv.) (Aizoaceae)
Sesuvium portulacastrum (L.) L. (Aizoaceae)
Sporobolus virginicus (L.) Kunth (Poaceae)
Stipagrostis prodigiosa (Welw.) De Winter (Poaceae)
Suaeda merxmuelleri Aellen (Amaranthaceae)
Zygophyllum simplex L. (Zygophyllaceae)