Coastal fore-dune zonation and succession in various parts of the world*

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Keywords: Coastal sand dune, Ecosystem succession, Phytogeography, Synecology, Vegetation zonation

Abstract

A table is presented of the most important species of the fore-dune complex in various parts of the world, representing all continents. The complex is divided into six zones or habitat types, which have proved to be widely applicable for this purpose. The zones are briefly described in terms of floristics, geomorphology, ecology (sand movement, salinity, organic matter) and climate. A major division is indicated between tropical (including subtropical) and temperate (including cold) regions. The former are subdivided into those with humid and those with arid climates, the latter into those with cool to warm-temperate and those with boreal to subarctic climates. The highest, most extensive and most complicated dune areas occur in those regions where the effects of disturbance by wind and fixation by plant growth are about equally strong. A number of species show the 'retraction phenomenon': a shift from a certain zone towards a more sheltered zone in an area with more harsh conditions (e.g. a shorter vegetation period). The filling of empty niches by introduced species (e.g. in connection with the scarcity of native tidemark species in temperate Australia) is also quite common. Most communities are rich in (sub)cosmopolitan species.

Introduction

Coastal plant communities in various parts of the world often have obvious similarities, partly due to specific environmental factors. In a previous paper (Doing, 1981a), a division of sand dune landscapes into a number of zones or habitat types has been proposed, with the aim of creating a frame of reference for more detailed studies of the relationship between geomorphology, plant communities, climate, etc., and for the understanding of the behaviour and ecology of species. It may be applied for the comparison of species niches in similar ecosystems in areas belonging to different phytogeographical and climatological regions. Although no studies in population dynamics and ecophysiology have been carried out, many problems relevant to these fields arise from it. Examples of this may be found in the abundance of nitrophilous species in various areas and their distribution throughout coastal zones (e.g. their tolerance to sedimentation and their degree of dependence on the presence of organic tidemark material). Since experimental or detailed studies are mostly limited to small areas, their range of applicability should be judged with the help of such a frame of reference. By means of regional comparisons, it is possible to take account of climatic variation, which is difficult to cope with by means of experiments.

To limit the scope of this paper, the 'fore-dune complex' has been chosen for a further elaboration of the original scheme (Doing, l.c.), and is presented in the form of a table with explanations (Table 1).

If the term 'fore-dune' is used in the sense of 'frontal dune' (as seen from the beach; cf. Bird, 1964), its position in the complete scheme of land-

* Nomenclature: see various regional references.

Vegetatio 61, 65–75 (1985).

scape zonation varies according to the climatic area as well as to the local history of the coastline, which makes it unsuitable for our purpose. Therefore, the term 'fore-dune complex' has been used to indicate the complete range of zones which may be present as a direct effect of recent, active transportation of sand and organic material perpendicular to the shoreline. In many areas, two dune ridges are present, varying in relative and absolute height (cf. the discussion on p. 9), and carrying at least two different plant communities. Because of the interdependence and interaction of the zones (numbered 1–6 in the table), the ecology of the communities and species growing in this situation can only be properly understood if they are treated as a whole. As an example, the situation in northern France (English Channel coast) is presented in Figure 1.

Explanation of the table

The fore-dune complex, which may be regarded as one geographical, geomorphological and functional unit (landsystem), is being divided into six zones, with distinctive plant communities. Major plant species are arranged according to their order of appearance in these zones in each area, starting from the beach. In the case of accretion, periods may occur when succession is possible, e.g. from tide mark ecosystems to embryonic dunes, and from low to higher dunes. Where erosion takes place, developments are possible in an inverse direction, or other zones arise, which are not being discussed here. In the former case, zones are often well developed, with clear boundaries between them. In the latter case, zones are more or less mixed with each other, and richer in species. As a general rule, however, the complete range of zones can only be constructed by studying a whole area, and in most places the zonation does not coincide with a succession. The meaning of the term 'rocky' in the first column is: relatively small sand dune areas in the vicinity of rocky coasts.

The taxonomic nomenclature is according to the majority of the referred publications, which appeared around 1970. Most of the species which occur only locally, have been omitted. In a full description of all zones (cf. Doing, 1981a, b), some of the species would be placed into a zone which does not occur in the table. On the other hand, a number of species are left out, which clearly have their optimum in those zones, or not in sand dunes at all.

It is very common, that species, which are major constituents of a more exposed zone, also occur (in lower numbers but with high frequencies, or in high number but with lower fertility or vitality) in one or more of the more sheltered zones. To avoid confusing repetitions, species are, as a rule, only mentioned in the first zone in which they are well developed. Exceptions are made for those species which are dominant or tend to form monospecific communities in two zones. These are mentioned in both zones. In each list, dominant species are mentioned first. The names of introduced species are placed between brackets.

Table 1 is far from complete. From the literature (e.g. phytosociological tables) it is often difficult to

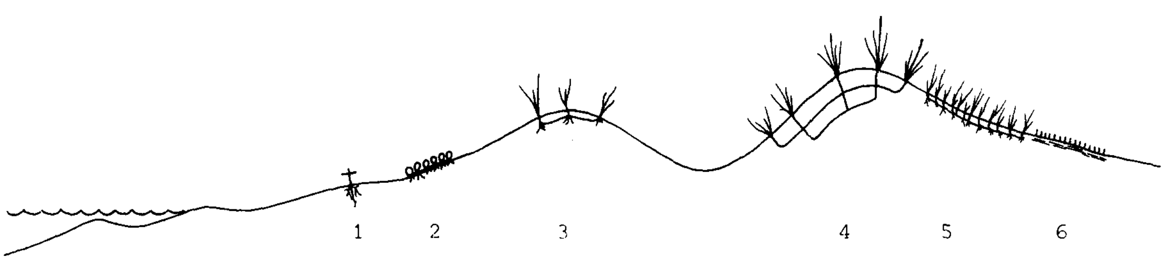

Fig. 1. Zonation in northern France (English Channel coast) along a stable coast.
Zones: 1. = *Cakile maritima* (only in favourable situations);
2 = *Honkenya peploides* (only in favourable situations);
3 = *Agropyron junceiforme* (minor part of sand fixed by vegetation);
4 = *Ammophila arenaria* (major part of sand fixed by vegetation);
5 = *Festuca rubra arenaria* (accretion up to few dm of sand per year);
6 = *Tortula ruralis* (accretion only few cm of sand per year).

Table 1.

Area, latitude, nature of coast and sand, aridity		1. Ephemerous tidemark communities	2. Perennial tidemark communities, normal height of dunes	3. Embryonic dunes or frontal ridge, normal height of dunes	4. Central fore-dune ridge, normal height of dunes	5. Sheltered zone	6. Pioneer communities in stabilized zone
Netherlands **North Sea** **sandy, calcareous**[1,40]	52° N	Cakile maritima	Honkenya peploides ½ m	Agropyron junceiforme Elymus arenarius 1 m	Ammophila arenaria Sonchus arvensis 5–10 m	Festuca rubra arenaria Rubus caesius Eryngium maritimum	Tortula ruralis Carex arenaria Viola curtisii Galium verum
East Frisian Islands (*D*), **W Jutland (DK)** **North Sea** **sandy, acid**[1, 2, 40]	53–57° N	Cakile maritima	*Honkenya peploides* ½ m	*Agropyron junceiforme* Elymus arenarius 1 m	*Ammophila arenaria* Ammocalamagrostis baltica Cirsium arvense Oenothera parviflora Eryngium maritimum 5 10 m	Festuca rubra arenaria Sonchus arvensis Lathyrus japonicus Hieracium umbellatum (Rosa rugosa)	Carex arenaria Corynephorus canescens Koeleria glauca Viola canina Jasione montana *Galium verum*
Scotland, SW Norway **Atlantic Ocean** **rocky, calcareous**[3]	56–59° N	Cakile maritima Salsola kali Atriplex laciniata Atriplex glabriuscula	Honkenya peploides Sonchus arvensis Elymus arenarius	Agropyron junceiforme 1 m	Ammophila arenaria Cirsium arvense 5 m	Festuca rubra arenaria Lathyrus japonicus	Tortula ruralis Camptothecium lutescens Carex arenaria Trifolium repens Galium verum
E Germany, S Sweden **Baltic Sea** **rocky, calcareous**[1, 4]	55° N	Cakile maritima Salsola kali	Honkenya peploides	Agropyron repens Elymus arenarius Sonchus arvensis	Ammophila arenaria Ammocalamagrostis baltica Eryngium maritimum Lathyrus japonicus Petasites spurius	Festuca rubra arenaria Hieracium umbellatum Calamagrostis epigejos (Rosa rugosa)	Carex arenaria Corynephorus canescens Koeleria glauca Jasione montana Galium verum
E Poland, Russia **Baltic Sea** **sandy, acid**[5, 40]	54–60° N	Cakile maritima Salsola kali		Elymus arenarius Honkenya peploides 2 m	Ammophila arenaria Ammocalamagrostis baltica Calamagrostis epigejos Petasites spurius 6 m	Festuca rubra arenaria Artemisia campestris Linaria odora Tragopogon floccosus	Carex arenaria Corynephorus canescens Hieracium umbellatum Jasione montana Helichrysum arenarium Cladonia sp.
Finland **Baltic Sea,** **Gulf of Bothnia** **rocky**[6]	61–65° N		Honkenya peploides Salsola kali Carex fusca 1 m	Elymus arenarius 3 m	Festuca rubra arenaria 2 m	Festuca polesica Festuca ovina 2 m	Carex arenaria Calamagrostis epigejos *Deschampsia flexuosa* 1 m
W Cotentin (F) **English Channel** **sandy, calcareous**[1, 7, 40]	49° N	Cakile maritima Salsola kali	Honkenya peploides	Agropyron junceiforme Elymus arenarius Eryngium maritimum Calystegia soldanella Euphorbia paralias 2 m	Ammophila arenaria 6 m	Festuca rubra arenaria Festuca juncifolia	Tortula ruralis Carex arenaria Vulpia longiseta
S Brittany, Vendée (F) ***Bay of Biscay*** **rocky, calcareous**[1, 8]	47° N	Cakile maritima Atriplex laciniata	Honkenya peploides Euphorbia peplis	Agropyron junceiforme Eryngium maritimum Calystegia soldanella 2 m	Ammophila arenaria Euphorbia paralias 5 m	Festuca rubra arenaria Galium arenarium Artemisia lloydii Diotis maritima Silene thorei	Tortula ruralis Carex arenaria Dianthus gallicus Helichrysum stoechas
Landes (F)[1, 9]	44° N	Cakile maritima	Honkenya peploides	Agropyron junceiforme *Eryngium maritimum* Calystegia soldanella Euphorbia paralias	Ammophila arenaria Diotis maritima	Festuca rubra arenaria Festuca juncifolia Galium arenarium Artemisia lloydii Astragalus bayonensis Hieracium eriophorum *Linaria thymifolia*	Carex arenaria Corynephorus canescens Helichrysum stoechas Cladonia sp.

Table 1. Continued.

Area, latitude, nature of coast and sand, aridity		1. Ephemerous tidemark communities	2. Perennial tidemark communities, normal height of dunes	3. Embryonic dunes or frontal ridge, normal height of dunes	4. Central fore-dune ridge, normal height of dunes	5. *Sheltered zone*	6. Pioneer communities in stabilized zone
W Portugal, W Spain Atlantic Ocean sandy, acid[10]	38–43° N	Cakile maritima Salsola kali Euphorbia peplis Polygonum maritimum	Honkenya peploides Eryngium maritimum Calystegia soldanella	Agropyron junceiforme Euphorbia *paralias*	Ammophila arenaria *Diotis maritima* Medicago marina Pancratium maritimum	Crucianella maritima Artemisia crithmifolia Armeria welwitschii Linaria broteri	Corynephorus canescens Helichrysum angustifolium Scrophularia frutescens Vulpia *alopecurus* Silene littorea Jasione lusitanica
S France Mediterranean Sea sandy, calcareous[1, 11]	43° N			*Agropyron junceiforme* Sporobolus arenarius Scleropoa maritima Cakile maritima Salsola kali (Xanthium macrocarpum) Polygonum maritimum Euphorbia *peplis* Eryngium maritimum Calystegia soldanella Euphorbia paralias Echinophora spinosa *Diotis maritima* 2 m	Ammophila ar. arundinacea Cyperus kalli Pancratium *maritimum* Medicago marina Anthemis maritima	Crucianella maritima Helichrysum stoechas *Centaurea aspera* Clematis flammula Teucrium polium Artemisia campestris Lotus cytisoides	Ephedra distachya Lagurus ovatus Vulpia fasciculata Bromus villosus Silene *italica* Saccharum ravennae
Greece Mediterranean Sea rocky, calcareous[12]	37–41° N		Euphorbia peplis Polygonum maritimum Anthemis muenteriana Anthemis tomentosa Cakile *maritima* Salsola kali Salsola soda Matthiola tricuspidata (Xanthium strumarium) 1½ m	Agropyron junceiforme Sporobolus arenarius Cyperus kalli (Xanthium macrocarpum) Eryngium maritimum Calystegia soldanella *Euphorbia paralias* Echinophora spinosa Diotis maritima Medicago marina 2 m	Ammophila ar. arundinacea *Cutandia maritima* Pancratium maritimum 7 m	Centaurea sonchifolia *Echium hispidum* Daucus pumilus	Lagurus ovatus Vulpia fasciculata Bromus villosus *Silene nicaeensis* Euphorbia terracina Hedypnois rhagadiolides
N Africa Mediterranean Sea rocky, calcareous[13]	32–36° N		*Cakile maritima* Salsola kali (Atriplex laciniata) Euphorbia peplis	Agropyron junceiforme Sporobolus virginicus Euphorbia paralias Pancratium maritimum	Ammophila ar. arundinacea Cyperus kalli *Calystegia soldanella* Silene succulenta Launea resedifolia	Crucianella maritima Teucrium polium	Ephedra fragilis Retama sp.
Senegal Atlantic Ocean sandy, calcareous arid[14]	15° N	*Alternanthera maritima*	Ipomoea pes-caprae Ipomoea stolonifera Canavalia rosea	Sporobolus spicatus Remirea maritima	Scaevola plumieri	Schizachyrium pulchellum Cyperus crassipes Tamarix senegalensis	Chrysobalanus icaco Diodia serrulata (Casuarina equisetifolia)
Equatorial W Africa[15]	5° N–5° S	Sesuvium portulacastrum Alternathera maritima	Ipomoea pes-caprae Phyloxerus vermiculatus Canavalia maritima Vigna marina	Sporobolus virginicus Remirea maritima	Scaevola plumieri	Chrysobalanus orbicularis *Chrysobalanus ellipticus* Dalbergia ecastaphyllum	Pandanus candelabrum Phoenix reclinata (Cocos nucifera)
SW + S Africa Atlantic Ocean arid[16]	24–34° S	Sesuvium *portulacastrum*	*Arctotheca populifolia*	Sporobolus virginicus Sebaca ambigua *1 m*	Agropyron distichum Ehrharta villosa *Eragrostis cyperoides* Aristida sabulicula Aristida namaquensis	Scaevola thunbergii	Myrica cordifolia Passerina sp.
Subtropical SE Africa or Indian Ocean[17]	28° S		Ipomoea pes-caprae Arctotheca populifolia *Canavalia maritima* Gazania rigens	Sporobolus virginicus	Scaevola thunbergii	Stipagrostis zeyheri Aristida junciformis Tephrosia purpurea Carpobrotus dimidiatus	Passerina rigida Chrysanthemoides *monilifera* Helichrysum ericaefolium (Casuarina equisetifolia)

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Kenya Indian Ocean rocky, calcareous[1,18]	4°S	Sesuvium portulacastrum	Ipomoea pes-caprae Atriplex farinosa Canavalia maritima (Tribulus terrestris)	Sporobolus virginicus Remirea maritima Lepturus repens 1 m	Scaevola plumieri Crotalaria retusa 2 m	Scaevola taccada Justicia flava Guizotia sp. Tephrosia purpurea (Casuarina equisetifolia)	Pandanus kirkii Pandanus rapaiensis Dodonaea viscosa Cocos nucifera
Tropical W Australia + Northern Territory Indian Ocean rocky, calcareous, arid[19]	17 25°S	*Sesuvium portulacastrum* (Salsola kali)	*Ipomoea pes-caprae* Canavalia maritima	*Spinifex longifolius* Sporobolus virginicus (Euphorbia atoto)	Acacia *sp.* Crotalaria cunninghamii	Casuarina equisetifolia	Triodia pungens
Temperate W Australia Indian Ocean sandy, calcareous[1,20]	30 33°S	(Cakile maritima) (Salsola kali)	(Arctotheca populifolia) (Euphorbia paralias) Atriplex isatidea	Spinifex longifolius Spinifex hirsutus Scirpus nodosus Carpobrotus glaucescens Sonchus megalocarpus (Oenothera drummondii)	Acacia rostellifera Scaevola crassifolia Olearia axillaris Rhagodia baccata Calocephalus brownii (Ammophila arenaria)	Banksia sp. Agonis flexuosa	Eucalyptus gomphocephala
S Australia Great Australian Bight rocky, calcareous[1,21]	32 35°S	(Cakile maritima) (Salsola kali)	(Arctotheca populifolia) Atriplex cinerea 1 m	Spinifex hirsutus Festuca littoralis Poa poiformis (Ammophila arenaria) (Euphorbia paralias) Scirpus nodosus *Carpobrotus rossii* Sonchus megalocarpus 5 m	Acacia sophorae Acacia ligulata Rhagodia baccata Calocephalus brownii Olearia axillaris Enchylaena tomentosa Correa alba Leucopogon parviflorus 10 m	Melaleuca lanceolata Melaleuca armillaris Pittosporum undulatum Casuarina stricta	Helichrysum apiculatum Crassula sieberana (Lagurus ovatus) (Aira praecox)
New South Wales Pacific Ocean rocky, acid[1,22]	35°S	(Cakile edentula) (Salsola kali)	(Arctotheca populifolia) (Euphorbia sparrmanii) Atriplex cinerea 1 m	Spinifex hirsutus Sonchus megalocarpus Calystegia soldanella Carpobrotus aequilaterus (Oenothera drummondii) 2 m	Acacia sophorae Hibbertia scandens Stephania japonica Scirpus nodosus (Hydrocotyle bonariensis) 6 m	Leptospermum laevigatum Phyllanthus gasstroemii Clematis glycinoides Casuarina glauca Viola hederacea	Tortella calycina Zoysia macrantha Crassula sieberana Polycarpon tetraphyllum
S Queensland Pacific Ocean sandy, acid[1,23]	27°S	(Cakile edentula) (Salsola kali)	Ipomoea pes-caprae	Spinifex hirsutus Canavalia maritima (Oenothera drummondii)	Acacia sophorae Hibbertia scandens Stephania japonica	Casuarina equisetifolia	Cupaniopsis anacardioides Pandanus peduncularis Thespesia populnea
Tropical Queensland Pacific Ocean rocky, acid[24]	17°S	Sesuvium portulacastrum	Ipomoea pes-caprae Glycine tomentella	Sporobolus virginicus Spinifex hirsutus Lepturus repens Canavalia maritima *Wedelia biflora* Remirea maritima (Euphorbia atoto)	Scaevola taccada (loc.)	Casuarina equisetifolia	Pandanus sp. (Cocos nucifera) Thespesia populnoides
SW Kyushu (Japan) Pacific Ocean rocky, volcanic[1,25]	33°N	Salsola komarovii Atriplex gmelinii	Calystegia soldanella Lathyrus japonicus Linaria japonica Glehnia littoralis	Carex kobomugi (non-flowering) 2 m	Carex kobomugi (optimal) 5 m	Ischaemum anthephoroides Wedelia prostrata Carex breviculmis	Racomitrium canescens Cladonia sp. Fimbristylis sericea
N Hokkaido (Japan) Pacific Ocean rocky, acid[1,26]	43°N	Salsola komarovii Atriplex subcordata	Senecio pseudo-arnica Sonchus brachyotis Honkenya peploides Artemisia montana	Carex macrocephala (non-flowering) Elymus mollis 1 m	Carex macrocephala (optimal) Lathyrus japonicus 2 m	Rosa rugosa Artemisa stelleriana	
North Carolina (U.S.A.) Atlantic Ocean sandy, acid[1,28]	35°N	Cakile edentula Salsola kali Euphorbia polygonifolia	Panicum amarum Panicum amarulum (Croton punctatus)	Uniola paniculata (non-flowering) Ammophila breviligulata 1 m	Uniola paniculata (optimal) Solidago sempervirens 2 m	Strophostyles helvola Muehlenbergia capillaris Oenothera humifusa Hydrocotyle bonariensis Cenchrus tribuloides	Andropogon scoparius Andropogon virginicus Fimbristylis spadicea
Massachusetts (U.S.A.)	42°N	Cakile edentula Salsola kali	Honkenya peploides	Ammophila breviligulata (non-flowering)	*Ammophila breviligulata* (optimal)	*Festuca rubra* Lathyrus japonicus	*Hudsonia tomentosa* Carex artitecta

Table 1. Continued.

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Atlantic Ocean rocky, acid[1, 29]		Euphorbia polygonifolia		2 m	Solidago sempervirens	(Artemisia stelleriana) (Rosa rugosa)	Andropogon scoparius Deschampsia flexuosa Cladonia sp.
E Canada Atlantic Ocean, Gulf of St. Lawrence rocky, acid[30]	51–55° N	Cakile edentula Atriplex sp. Polygonum sp.	Honkenya peploides Mertensia maritima Salsola kali ½ m	Elymus mollis Senecio pseudo-arnica Sonchus arvensis Oenothera parviflora 3 m	Ammophila breviligulata Lathyrus japonicus 15 m	Festuca rubra Carex silicea Solidago sempervirens Solidago bicolor Achillea millefolium (Artemisia stelleriana)	Anaphalis margaritacea Deschampsia flexuosa Cladonia sp.
New Quebec (Canada) Hudson Bay[31]	55–60° N		Honkenya peploides	Elymus mollis (non-flowering) Festuca rubra arenaria Mertensia maritima 2 m	Elymus mollis (optimal) Lathyrus japonicus Tanacetum huronense 4 m	Trisetum spicatum Achillea borealis Stellaria subvestita Campanula rotundifolia Astragalus alpinus	Racomitrium canescens Rhytidium rugosum Potentilla tridentata Cladonia sp.
Iceland N Atlantic Ocean rocky, volcanic[32]	64° N	Cakile edentula	Honkenya peploides Mertensia maritima ½ m	Elymus arenarius (optimal) 5 m	Elymus arenarius (non-flowering) Silene maritima 1½ m	Festuca rubra cryophila Carex capillaris	*Tortula ruralis* Racomitrium canescens Armeria maritima Rumex acetosella Cardaminopsis petraea
N Norway Norwegian Sea rocky[33]	70° N	Cakile edentula	Honkenya peploides Mertensia maritima Polygonum raii Atriplex lapponica	Elymus arenarius (non-flowering)	Elymus arenarius *(optimal)* Lathyrus japonicus	Festuca rubra arenaria Solidago virgaurea Achillea millefolium	
Florida (U.S.A.) Atlantic Ocean sandy, calcareous[34]	28° N	Sesuvium portulacastrum Cakile edentula Atriplex laciniata	Ipomoea pes-caprae Ipomoea stolonifera Panicum amarulum *(Croton punctatus)* ½ m	Uniola paniculata (non-flowering) Scaevola plumieri Canavalia rosea 1 m	Uniola paniculata (optimal) Andropogon virginicus 5 m	Andropogon glomeratus Muehlenbergia capillaris Schizachyrium scoparium	Sabal palmetto Coccoloba uvifera Opuntia stricta Suriana maritima Tournefortia gnaphalodes Cladonia sp.
S Florida (U.S.A.), Mexico, Gulf of Mexico rocky, calcareous[35]	24–26° N	Sesuvium portulacastrum Amaranthus greggii Cakile lanceolata	Ipomoea pes-caprae Ipomoea stolonifera Panicum amarulum *Phyloxerus vermicularitus*	Sporobolus virginicus Canavalia maritima Canavalia lineata Canavalia obtusifolia Diodia serrulata	Scaevola plumieri Suriana maritima Tournefortia gnaphalodes	Cenchrus tribuloides Borrichia arborescens	Coccoloba uvifera Thespesia populnea
Leeward Islands, Venezuela, Caribbean Sea rocky, calcareous[36]	12° N	Sesuvium portulacastrum Heliotropium curassavicum	Ipomoea pes-caprae Phyloxerus vermicularis	Sporobolus virginicus Canavalia maritima	Aristida venezuelae Suriana maritima Tournefortia gnaphalodes	Dactyloctenium virginicum	Prosopis juliflora Erythroxylon sp. Coccoloba uvifera Cakile lanceolata
Washington, Oregon (U.S.A.) Pacific Ocean rocky[1, 27]	43–48° N	Cakile edentula	Lathyrus japonicus Abronia umbellata	Elymus vancouveriensis Elymus mollis Calystegia soldanella	Carex macrocephala Poa macrantha Polygonum paronychia Lathyrus littoralis Abronia latifolia Glehnia leiocarpa Angelica hendersonii Ambrosia chamissonis Tanacetum camphoratum (Ammophila arenaria)	Festuca rubra Lupinus littoralis Fragaria chiloensis	Racomitrium canescens Anaphalis margaritacea
Chile Pacific Ocean sandy, calcareous, arid[37]	27° S			Nolana divaricata Tetragonia maritima Alona carnosa *1 m*	Ephedra cf. breana Skytanthus carnosus *4 m*	Suaeda cf. fruticosa Spergularia arbuscula Frankenia glabrata *Heliotropium* linariaefolium Cristaria pinnata	

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Chile Pacific Ocean rocky, calcareous[38]	30–42° S			Nolana paradoxa (30 45° S) (Ambrosia chamissonis herbaceous 28 42°) Polygonum sanguinaria (30 44°) Salsola kali	(Ambrosia chamissonis woody) Cristaria glaucophylla (27 32°) Distichlis spicata (30 42°) Panicum urvilleanum (35–42°)	Carpobrotus chilensis (28–40°) Solanum heterantherum (30–33°) Senecio munnozii (30 33°) Poa aff. lanuginosa (32 42°) Carex pumila (32 44°) Fragaria chiloensis (37 44°) (Prosopis chilensis)	Chorizanthe vaginata (27 42°) Hypochaeris toltensis (33–42°) Euphorbia portulacoides (33 42°) Calystegia soldanella Oenothera stricta Chamissonia dentata (Lagurus ovatus)
Hawaii (U.S.A.), Polynesia (F), Pacific Ocean rocky, calcareous[39]	20° N–20° S	Sesuvium portucalastrum	Ipomoea pes-caprae Nama sandwicense Tribulus cistoides Vigna marina Hedyotis romanzoffii	Lepturus repens Sporobolus virginicus	Scaevola frutescens Vitex trifolia		Cocos nucifera Thespesia populnea Acacia simplicifolia (Coccoloba uvifera) (Casuarina equisetifolia)

[1] Field observations by the author.
[2] Ellenberg, 1978; Heykena, 1965.
[3] Gimingham, 1964; Tüxen, 1967.
[4] Olsson, 1975; Passarge & Passarge, 1973.
[5] Wojterski, 1964.
[6] Lemberg, 1933.
[7] Turmel, 1949. The zonation is very similar along most of the coasts of England, Wales and Ireland: van der Maarel & van der Maarel-Versluys, 1963.
[8] Vanden Berghen, 1958, 1965.
[9] Vanden Bergen, 1964–65.
[10] Braun-Blanquet *et al.*, 1972; Rivas-Martinez, 1972.
[11] Kühnholtz-Lordat, 1923; Pignatti, 1959a & b.
[12] Horvat *et al.*, 1974; Lavrentiades, 1964, 1976; Oberdorfer, 1951–52; Pavlidis, 1976.
[13] Vanden Berghen, 1979b.
[14] Adam, 1975; Vanden Berghen, 1979a.
[15] Knapp, 1973; Schnell, 1971.
[16] Knapp, 1973.
[17] Weisser, 1978.
[18] Knapp, 1973.
[19, 20, 21, 22, 23, 24] Beadle, 1981.
[21] Also Specht, 1972.
[25, 26] Ohba *et al.*, 1973.
[27] Franklin & Dyrness, 1969; Knapp, 1965; Wiedemann *et al.*, 1969.
[28] Doing, 1981a; Godfrey & Godfrey, 1976.
[29] Doing, 1981a.
[30] Grandtner, 1968, 1974, 1979; Lamoureux & Grandtner, 1977; Thannheiser, 1981a, b.
[31] Bournerias & Forest, 1975.
[32] Tüxen, 1970.
[33] Thannheiser, 1974.
[34] Coastal Plants of Florida, 1979; Knapp, 1965; Kurz, 1942.
[35] Knapp, 1965; Sauer, 1967.
[36] Lasser & Vareschi, 1957; Stoffers, 1980.
[37, 38] Kohler, 1970.
[39] Denizot, 1975; Knapp, 1965.
[40] Walter, 1968; Westhoff & Schouten, 1979; also for information on areas not treated in the table.

derive the correct position of species in the zonation.

Vegetation structure is extremely variable, even within the same community, and in many publications it is not well described. For these reasons, it is not mentioned in Table 1.

General conclusions

1. The division of the fore-dune complex into the 6 zones, distinguished in Table 1, has a worldwide applicability, and is used in a similar way by many authors, although in many cases the complete range has to be constructed from various examples or papers (e.g. Gimingham, 1964; Heykena, 1965; Ohba *et al.*, 1973; Thannheiser, 1981b; Wojterski, 1964). However, the clearness of a certain zone, morphology and height of the dunes, sharpness of boundaries and structure of the vegetation may vary considerably with geographical situation and general climate.

2. The main distinction is into areas with a tropical (including subtropical) and those with temperate (including cold and most of the Mediterranean) climates. In both cases, there are a number of subcosmopolitan or widespread species, particularly among the dominants of plant communities. Some of these are neophytes in part of their present area, e.g. *Ammophila arenaria* in North America and Australia (from Europe), *Xanthium* sp. in S Europe (from America), *Cakile maritima* (from Europe), *C. edentula* (from N America) and *Arctotheca populifolia* (from S Africa) in Australia, *Artemisia stelleriana* in N America (from E Asia) and *Ambrosia chamissonis* in S America (from N America).

3. Both major areas can be divided into two parts, in the following way:

a. The tropical sand dunes in humid regions are generally low, with mainly low grasses (*Sporobolus*!) in the front ridge, and woody species (*Scaevola*!) in the second ridge and further inwards. Some of the major species (*Sesuvium*!) also occur in salt-marsh landscapes. Physiognomically, most temperate Australian dunes (*Spinifex, Acacia*) belong to this category. In arid regions, dune species are either halophytes (from taxa like *Suaeda, Tamarix, Frankenia,* etc.) or grass taxa which also occur in desert dunes away from the coast (e.g. *Aristida*). In the inner zones, dunes are high, with scarce or no vegetation.

b. In the northern hemisphere, the temperate region is rich in extensive dune areas, with *Ammophila* as by far the most prominent dune-building taxon, mostly supported by *Agropyron* in the front ridge. A complete range of environments (Doing, 1981a) occurs more frequently here than in the other regions. In cold (boreal and subarctic) regions, dunes are mostly low, and *Elymus* is the main dune-building genus. There is a range of intermediate forms between various types of tidemark and dune ecosystems. Slow mineralization of organic matter is probably a reason for this.

4. There are many examples of geographically vicarious species within a genus, or vicarious genera within a family, occupying similar niches. The most important genera are: *Cakile, Festuca, Vulpia, Ammophila, Carex, Silene, Linaria, Casuarina, Canavalia, Glehnia, Oenothera, Helichrysum, Xanthium, Artemisia* and *Scaevola*. Vicarious genera belong e.g. to the families Gramineae, Cyperaceae, Aizoaceae, Caryophyllaceae, Convolvulaceae, Papilionaceae, Umbelliferae, and Compositae. A large majority of the species, mentioned in Table 1, and many others, belong to these taxa.

5. Some of the taxa are very consistent in their preference for a certain zone, e.g. *Cakile maritima* (zone 1), *Honkenya peploides* (zone 2) and *Festuca rubra* (zone 5). Others, equally occurring in various areas, tend to shift from one zone to another. Fairly common is a kind of behaviour, which might be called 'retraction phenomenon': a species (or group of species) retreats into a more sheltered zone away from its climatic optimum, where conditions are more extreme in one or more respects. Examples can be derived from Table 1 by comparing the columns in which these species (e.g. *Eryngium maritimum, Calystegia soldanella*) are mentioned for different areas. Salt tolerance and the force of blowing sand – especially during the main season for vegetative growth – are factors likely to explain this. The ability of a number of species which do not belong to the standard list of sand binders, to act as initiators for dune formation in areas sheltered by rocks, fore-dunes or artificial screens (e.g. *Cakile maritima, Salix arenaria, Spartina* sp., *Empetrum nigrum*) may be explained in the same way.

Relationships between geomorphology, plant ecology and climate

The 'standard zonation' is optimally developed in warm-temperate, humid climates and on shores, exposed to ocean tides and winds. Even here, it is often only found in the most favourable situations. The development of tidemark zones is favoured by the vicinity of rocky shores with abundant plant and animal life. Calcareous sand is favourable for species richness, especially among woody species.

Towards the colder as well as the tropical regions, dune formation becomes less pronounced. In the former case, the sand-binding capacity of plants decreases, probably because of the shorter duration of the growing season. In Europe and North America, *Ammophila* disappears towards the north, and is gradually replaced by *Elymus* as the major sand-binding species (Thannheiser, 1981b, c; Tüxen, 1966, 1970). Dunes are lower, even where wide dune areas occur. In formerly glaciated regions, raised shorelines are common, and here less time has been available for the formation of continuous dune areas. In the coldest regions, ice, snow and frozen soils severely limit the period during which sand may be blown. At the same time, there is a decreasing degree of salinity within comparable zones.

In humid tropical areas, sand transport by wind is limited (Bird, 1964). In climates where wind velocities are generally low, this may be a sufficient explanation for the scarcity of high or wide dune areas. Moreover there is a difference between the height of summer and winter spring tides which is often much less than in the 'forties' and 'fifties' (northern and southern latitude), where many aspects of the zonation of dune and salt-marsh landscapes can be explained, starting from this. A very long growing season is favourable for the development of relatively dense, woody, salt-tolerant vegetation zones close to the shoreline. This can be observed in dunes, on rocky coasts as well as in mangroves and salt marshes. It is clear, that this must hamper dune formation and erosion. Even in an equatorial climate, high sand dunes may occur, if there is an arid season, e.g. in northeastern Kenya.

We may conclude, that the most impressive foredunes and parabolic dunes, directly derived from them, occur where the struggle between wind and vegetation is undecisive during longer periods.

Apart from being more susceptible to local factors, tidemarks develop along different lines, often resulting in tendencies opposite to those of sand dunes.

There is some confusion in the literature about the independence of ephemeral tidemark communities, consisting of annual species (e.g. Oberdorfer, 1952). Partly this is due to the vulnerability of these communities and to the local history of coastlines. Because of rising sea levels, a retreating coast, not permitting the development of these communities as a well-separated zone, is the most common situation. Even where conditions are more favourable, they often occur only in some years, or each year in different places. This means, that authors working in the same region but in different years, may come to different conclusions. However, there are apparently two cases in which they are missing for climatological reasons: very cold areas (generally unfavourable for the maintenance of annuals) and areas with hot, dry summers, which create extremely harsh conditions on the beach. Species like *Cakile maritima* still occur in such climates, but they are found further inwards, profiting from the protection of perennial grasses (e.g. *Elymus*). This is an example of the 'retraction phenomenon', mentioned before.

Where tides are more or less concentrated on the same level, which is the case where storm surges are either quite frequent or very rare, various tidemarks tend to overlap with each other or even with the zone of embryonic dunes. In connection with this, permanent tidemark communities are missing as a separate zone along parts of the Baltic Sea, the Mediterranean Sea and in Chile. In temperate Australia, native tidemark species are scarce and do not form plant communities, leaving an empty niche which is filled by European, North American and South African species. The most varied tidemark complex described is that of eastern Canada (Thannheiser, 1981a).

The relationship between embryonic dunes and the central fore-dune ridge is also variable. Wide, high beaches carry a zone of small crescentic dunes without vegetation, situated between zones 1 and 2 or 2 and 3. Where sufficient sand is available, there may be two parallel ridges with vegetation (e.g. in W France (Fig. 1)). Normally the inner ridge is the highest and best vegetated one, but the opposite is also possible (e.g. on Iceland). In each area and each zone, there is mostly only one grass or *Carex* species, building the majority of the dunes. Most of the other species may be interpreted as indicators of temporary chemical enrichment, originating from tidemark material or salt spray, and missing in many or even in most places. On this basis, it is possible to make a distinction between monospecific and 'enriched' communities, which has largely been neglected in phytosociological literature (Doing, 1981a). This concerns mainly the species *Agropyron junceiforme, Spinifex hirsutus, Sporobolus virginicus, Carex kobomugi, C. macrocephala, Uniola paniculata, Ammophila arenaria, A. breviligulata, Scaevola plumieri* and *Acacia sophorae.*

On barrier islands along flat coasts, especially where hurricanes occur frequently (e.g. the 'Outer Banks' of North Carolina), fore-dunes remain low because of the phenomenon of 'overwash', creating another special type of habitat (e.g. with *Spartina patens*), described by Godfrey & Godfrey (1976).

In some areas, the main species in zones 3 and 4 is the same. In tropical and subtropical areas and in temperate Australia (with very mild winters, also indicated by the presence of mangroves), the major fore-dune ridge is colonized by woody species.

Zones 5 or 6 may remain without plant communities in hot, arid regions (Senegal (Adam, 1975), N Chile (Kohler, 1970)) or carry communities which are not specific for sand dunes (N Norway (Thannheiser, 1974)). The sheltered zone (5) is often very different from the other zones and its communities are quite distinct, with several characteristic species, e.g. with local endemics in SW France (e.g. *Astragalus bayonensis, Linaria thymifolia,* Vanden Berghen, 1964-65). This is somewhat underestimated by some authors.

In many dune areas, the fore-dune complex represents only a minor part of their total surface. There are many other differences between such areas than could be discussed here. However, the occurrence of the other zones is more limited to certain climatic or geographic areas, and the number of publications in which they are described, is limited.

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Accepted 18.4.1984.