A comparative scheme of dry coastal sand dune habitats, with examples from the eastern United States and some other temperate regions

by

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Contents

1. Introduction

Coastal sand dunes in large parts of the world have much in common as an environment for plant life. The action of surf and wind results in relatively homogeneous particle size of the sand, irrespective of the composition of local sediments or rocks. The sand on the beach, from which dune formation originates, is enriched with salts, nutrients and organic matter from the sea. The high permeability of the substrate, caused by its coarse texture and granular structure, results in strong drainage (loss of water in the subsoil) and leaching, so that, more or less independant of the local climate, there is a tendency towards the formation of arid ecosystems, and in old dune systems to podsolic soils (BURGESS and DROVER 1953). In addition to this, the proximity of the sea acts as a buffer against climatic extremes, e.g. hot summers or cold winters. High air humidity and the influence of salt spray are also levelling factors in this respect. As far as dune formation is influenced by sea level changes, especially during the last c. 5000 years worldwide similarities in the morphology and age of dune areas on different coasts may be ascertained.

The flora of mobile sand dunes has a very specialised character nearly everywhere, resulting in the predominance of species not occurring in other types of environment. The number of species is mostly low, even in floristically rich regions. Because of the similarity of environments over large geographic areas, as well as the efficiency of propagule dispersal by sea water, wind or migratory birds, worldwide comparisons of sand dune vegetation are more relevant than in the case for most vegetation types. Some species (e.g. *Salsoli kali* in temperate and *Ipomoea pes-caprae* s.l. in tropical areas) (e.g. *Salsola kali* in temperate and *Ipomoea pes-caprae* s.l. in tropical areas) have very large areas indeed. Others have been introduced by man for specific purposes (e.g. *Ammophila arenaria*) or accidentally (e.g. *Cakile* sp.) far outside their original areas. Even where species are different, certain taxonomic groups are found in similar roles along coasts which are geographically far apart, e.g. *Chenopodium* or *Atriplex* and *Euphorbia* sp. on the beach, or *Rosa* sp. on fixed dunes. Such similarities are even more obvious when life forms are taken into account. Perennial, evergreen grasses and sedges which are able to form new sprouts and roots as they are being buried by fresh sand

are the principle dune builders nearly everywhere, often accompanied by more or less succulent *Asteraceae, Brassicaceae, Fabaceae, Apiaceae* etc. Various pioneer shrubs are able to fix atmospheric nitrogen via their root nodules and associated micro-organisms. The fixing and simultaneous leaching of the dune surface is often indicated by lichens.

It is the purpose of this paper, to propose a framework for comparisons of temperate coastal sand dune zonation and habitat types on coasts which are far apart, viz. the eastern U.S., Europe, Japan and Australia. Although existing literature was essential for this compilation, no regions are described which were not studied by the author. Even where detailed descriptions were available, it proved to be difficult or impossible to extract the kind of information needed for this purpose from the literature without personal familiarity with the area.

Possible starting points for such comparisons could be latitude, similar climate, taxonomic or ecologic relationships, composition of plant communities, ecosystems succession, zonation, or geomorphology.

From what is known about the distribution of coastal plants and plant communities, it is clear that comparable major changes, such as between communities indicative of cool and warm temperate zones, or between herbaceous and woody vegetation within a dune system, cannot be related to a single geographical, climatic or other environmental factor. For an evaluation of the total cumulative effect on vegetation of all relevant factors, the starting point must be the major boundary lines between plant communities based on their structure, floristic composition and successional status.

Classifications permitting comparisons of well defined plant communities on different continents are rare in the literature. The only relevant examples based on a uniform approach are phytosociological units according to BRAUN-BLANQUET (e.g. GEHU and TÜXEN 1975). However, analyses of American coastal dune vegetation available at present are not sufficient to apply this type of classification. Apart from this, it seems doubtful whether the delimitation of communities on the basis of characteristic and differential species will solve our problem. Sufficiently detailed field studies have shown various interesting examples of a shift in the optimal occurrence of widespread species on different coasts. Species like *Cakile maritima* and *Salsola kali*, which form separate (though relatively unstable) communities along western

European drift lines on sandy beaches, occur along most Mediterranean coasts as dune plants, beach vegetation being generally absent there, probably because of arid conditions during summer (OBERDORFER 1952). DOING (1960) mentions a "retraction phenomenon" for various groups of species, going along European atlantic coasts from south to north. Species like *Eryngium maritimum* and *Calystegia soldanella*, which grow abundantly in exposed places e.g. in the foredunes of "les Landes" (southwestern France), show a gradual retreat into more sheltered locations e.g. in the Netherlands, which is obviously also related to climatic differences. Thus, in different parts of the coast, the same species may have their optimum not only in different geomorphological zones, but also in different plant communities according to the BRAUN-BLANQUET classification. There are many other examples which show that "characteristic species" are linked to a certain plant community only within a limited phytogeographic area. Their status as such can never be established "once and for all" or for the whole area of a certain community type, otherwise circular reasonings between the concepts of species status and community composition are unavoidable. A comparable example is the behaviour of *Spartina patens* along the atlantic coast of the U.S.: in the north it is largely a salt marsh species, in the south it is also the most important species in "overwash" areas of sand dunes (GODFREY 1970). *Sporobolus virginicus* also shows this type of shift, e.g. along the eastern coasts of Australia. Far from being regarded as annoying exceptions in an otherwise neat classification, comparisons should take full account of such interesting phenomena. On the other hand, insufficient attention is sometimes given to the absence of a part of the "characteristic species combination" in certain, often well defined forms of a phytosociological unit. Monospecific communities are commonplace in extreme environments, and consequently cannot be classified on a purely floristic basis.

Because of the many similarities already mentioned, which exist between coastal sand dunes even in areas which are geographically far apart, it is possible to design a series of "standard conditions" which occur almost universally in this type of landscape. These may be preliminarily described as combinations of local geomorphological and mesoclimatological zones, soil types and plant communities based on structure as well as floristic composition and successional position. In the following pages, propositions will be

made for the distinction of such a series as a means to compare parallel "habitat types" or ecosystems in various parts of the world. After taking note of the examples in the last part of the paper, it is hoped that the meaning of the concept of "habitat types" will be clearer.

2. General description of dune landscape elements

Dune landscapes, especially in more or less humid climates and where the foredune sand is calcareous, are very complicated mosaics of geomorphological elements, soil and vegetation types. These mosaics can only be properly understood on the basis of detailed local descriptions and with the help of succession and other historical studies and of large scale maps, combined with an all-round knowledge of the ecology of at least the dominant species. It is not the purpose of this paper to explain such mosaics in any detail. It is hoped, however, that the standard landscape elements described here will help in analysis of local dune systems in such a way that a comparison of vegetation types in different regions will be facilitated.
The elements are distinguished on the basis of field experience and on the literature, and are intended as a synthesis of the major habitat types for plant species and plant communities in coastal sand dunes in general.

1. The beach and drift line

In most areas, the beach is an environment, hostile to higher plant life. Where winds are not too strong, humidity is high and especially where organic material (mostly in the form of a "tide mark") is present, plant communities may develop which are in many cases highly specific for this zone, at least within a certain climatological area.
a. The position of drift lines is often erratic because it depends on the relatively recent occurrence and severity of storms, and their importance as a substrate for plant life is of short duration. Under such circumstances, species poor communities of salt tolerant, mostly more or less succulent annual herbs, occur mainly where a strip of tide mark material high on the beach is blown over by a thin layer of sand.

b. Along the coast there are sometimes certain places (e.g. where the foredune ridge is interrupted or at the extremity of a barrier island) where tide mark material is deposited year after year in approximately the same locality. On tropical beaches this is often the normal situation throughout. Here, perennial and slightly less tolerant annual species may develop, which are often also able to catch a certain amount of moving sand and in this way initiate the formation of embryonic dunes. The latter case represents an intermediate between types 1 and 2.

2. Embryonic dunes

a. On wide beaches, low ephemerous dunes may be formed which are too unstable to carry vegetation. Under relatively favourable conditions, colonisation of such dunes is possible by species resistant to salt and blowing sand. These are nearly always perennial graminoids with low density and underground vegetative reproduction. The embryonic dunes which are formed in this way have crescentic shapes in some areas, or those of low (frequently interrupted) foredune ridges (e.g. up to 2 m high) parallel to the high water line in other areas. Where active dune building takes place, most communities are monospecific.

b. In the presence of organic material, such as after storm damage or deposition of tide mark material, additional species are frequently found. In addition to the species of elements 1a or b, some more or less succulent herbs are specific for this zone. These "facultative" members of the community often have smaller distributional areas than the dominant species and can be used as "geographic differential species", but not as "characteristic" species.

3. Main foredunes ("yellow dunes"

a. Even where zones 1 and 2 are well developed, most of the sand which moves landinwards from the beach cannot be permanently fixed in these zones because of their low height and vegetation cover. The same situation exists to a considerably higher degree for the foredune ridge which is often uninterrupted and 5-10 m high. In typical cases, flooding by sea water does not occur in normal years. Vegetation structure is similar to that in zone 2a, but

height and density of the graminoid synusia is much greater. Communities in actively onblowing sand are also normally monospecific, and the species may be the same on those of zone 2a in the corresponding area. In warm and humid climates, however, woody species may be present or even dominant here.
b. Under similar conditions as mentioned under 2b, additional species may occur in parts of the foredune ridge where organic material accumulates.

4. *Sheltered zone immediately behind foredunes*

Most of the sand and tide mark material which has not come to rest in one of the former zones, is deposited in this zone because of the reduction of the wind force by surrounding dunes. As in zones 1-3 vegetation is regularly buried by fresh, dry sand, and the soil profile may contain some organic matter down to several meters although usually there are only traces at the surface. The zone is nearly always developed adjacent to the leeward side of the main foredune ridge and sometimes also behind this in form of a more or less narrow belt of low, irregular dunes. As in former zones, there is usually a relatively coarse vegetation pattern with sand binding graminoids and herbs dominant, although small annuals, chamaephytes and even dwarf shrubs may play an important role in this zone. Monospecific communities are exceptional. Flora and vegetation vary more with climate than in the former zones.

Between the zones as discussed up to this point, there is not usually a successional relationship. All carry pioneer communities. On a stable coast, their spatial pattern is to be considered as a "normal" arrangement of landscape elements, to be explained as a series of facets of a "geosystem" (DOING 1979). Only where the coast is extending or retreating, are zones converted into others zones (DOING 1973). Many landscapes (e.g. cliffed coasts) in which the standard arrangement as discussed here is not present can be explained on this basis without serious difficulties.

5. *"Overwash" sandy flats*

In certain situations, such as on a wide beach or primary valley with low or interrupted foredunes,or between a dune and a salt marsh area, more or less flat sandy areas occur which are not shaped primarily by the wind but by the streaming water of high tides transporting sand. The surface is too high

for regular deposition of silt or for vegetation to be determined by ground water influence. Vegetation can best be considered as part of the dune xerosere. This landscape element has not received much attention in the literature (see, however, GODFREY 1970) but it is of considerable interest and in many areas indicated by particular species (mostly large perennial grasses), which must be tolerant to occasional flooding by sea water.

6. Salt spray vegetation

Although salt spray may be a major factor for the explanation of the specific character of coastal sand dune vegetation in general (OOSTING and BILLINGS 1942), specially in climates with more or less dry periods, a subdivision of landscapes as proposed here must be based primarily on the nature and mobility of the substrate. In this context, zones 1-5 (pronouncedly) and 7-9 (partly) are characterised by instability of the soil surface, and zones 10-14 by primary or secondary succession and development of the soil profile. However, there are often parts of a sand dune area close to the beach where the soil surface is stable, the moisture holding capacity of the soil is not very low but the influence of wind and salt spray is such that further succession is seriously retarded. Vegetation in these places is not different in principle from that of dry cliffs under the influence of salt spray and some of the highest salt marshes. Whether it is herbaceous or woody, depends on the climate and on the local flora.

7. Open pioneer dune shrub or woodland

Woody species are generally too vulnerable to be present in the most extreme environments. In most temperate sand dunes, dune shrublands are found as successional stages, following ecosystems as mentioned here for zone 3 (main foredune ridge). In undisturbed dune areas, this development takes place mainly where the coast is extending, and existing dunes are cut off from the stream of sand being blown in from the beach. (In many cases, the former beach is then transformed into a "primary valley", and succession in the hygrosere is initiated, which is not being discussed here). A certain amount of "richness" (e.g. provided by decomposing organic matter), indicated by a not too low pH, seems to be a prerequisite for shrub development. The previous pres-

ence of a herbaceous type of vegetation with roots penetrating deeply into the dune (often caused by repeated burying with fresh sand) is an important factor for the establishment of pioneer shrubs. The occurrence of this condition is not limited to the foredune ridge. Local destruction of the vegetation at any place in a dune area (e.g. by grazing or by storm surges creating a cliff) may lead to "rejuvenation" and (where the right amount of sand accumulation takes place, which is often in the order of 0.1-1 m/year), to the re-establishment of a type of vegetation similar to that present in zone 3a. This is one of the main reasons for the occurrence of dune "mosaics" in general, and for the possibility of the establishment of pioneer shrubs scattered throughout dune areas in particular.
The presence of dune shrubs and their position in succession series varies considerably, depending on climatic and soil conditions. In most areas there is only one prominent species in this zone.

8. Dry, short, open dune grassland

Relatively species rich communities, mainly consisting of small annual as well as perennial graminoids and herbs, sometimes rich in bryoids and lichens, are present in most (but not in all) fixed dune areas. Where they are present only in older dunes as a "grazing climax", although sometimes covering large surfaces, they cannot be considered as an essential link in dune succession and zonation and will not be further discussed here. The species poor communities of acid sterile sands will be discussed under point 9. The remaining communities occupy those environments which are not filled by one of the other types, and fall mainly into the following two categories.
a. In an accumulation zone, similar to that described under 4, but with sand accretion of only ca. 1 to several cm per year, open pioneer communities of dwarf plants may be developed. Even where the sand is poor in minerals, it is never acid because of the presence of shell fragments from the beach or from the subsoil of "blowouts". Along cliffed dune coasts with prevailing winds from the sea, communities of this type may occur behind the cliff in a zone several hundreds of meters wide, mostly mixed with shrubs or other, more closed communities.
b. As a somewhat more advanced succession stage, moss (and sometimes lichen)

rich communities are present on fixed surfaces in some areas with calcareous sand, following those of zone 4 or 8a. The soil is usually completely covered with vegetation.

9. *Open, sterile sand (e.g. blowouts) in secondary or older dunes ("gray dunes")*

Where vegetation is damaged, destruction by wind may take place in all dune zones (see under 7). This may lead to parabolisation and formation of "secondary valleys" by deflation down to the capillary level of the ground water. Hygrosere succession in these valleys is frequently taking place along lines different from those in primary valleys. Since only xerosere elements are discussed here, we are only concerned with the smaller blowouts with a "hollow" bottom. The sterility of the substrate, which is dry and contains no effective amounts of organic matter, combined with extreme temperature fluctuations and the occurrence of whirlwinds which tend to remove sand, seeds and other propagules, causes these places to be a very unfavourable environment for colonisation by plants. There is often no vegetation present. In most areas, specific communities are found in the less active or smaller blowouts, poor in species and often partly consisting of lichens and other plants which are attached to rather than deeply rooting in their substrate. Species, resistant to deflation are everywhere smaller in number than those, adapted to accumulation of sand.
Especially in older, leached dunes, parabolisation may not be the final stage of geomorphological development. Quasi-total destruction of the plant cover results in the formation of circular, transverse or oblique dunes (DEPUYDT 1972, VAN DIEREN 1934, PAUL 1944, 1953, PANNEKOEK 1936) which may move inland over distances of many kilometers ("Wanderdünen") and grow up to 100 m high in windy climates where sufficient sand is available. Where they are colonised by natural vegetation, this is mostly similar to that of zone 3a at the tops and to that of zone 8 (calcareous sand) or 9 (acid sand) on the slopes. Of course, older dunes may be covered by later stages of succession, e.g. dune heaths (14) or maritime forests (12), some of which may be favoured by the decrease of salt spray influence with increasing distance from the beach.

10. Ecosystems with increased decomposition of organic matter in the topsoil

A peculiar type of environment is created where dead plant material is mixed with the top soil, especially when the sand is calcareous or where the process is combined with a salt spray effect. Apparently, an increased rate of mineralisation of this organic matter under basic conditions is responsible for the specific plants and vegetation types found in such places, although existing methods of soil analysis do not seem adequate at present to describe how and explain why this situation is so unique. It is found either where parabolisation is actively going on and relatively dense vegetation has been recently buried by fresh sand, or where woody vegetation is dying off. Two, often quite different sub-groups can be distinguished. In both cases the loss of organic material is linked with retrogressive succession of ecosystems.

a. Young, calcareous dunes, mostly closely behind the foredunes or under the influence of salt spray. In regions with dry climatic periods, succulents are prominent here. As long as pH is high, mineralisation of organic matter is nearly complete and scarcely any stable humus is formed.

b. Older dunes, where woody vegetation is or has been present. A development from herbaceous communities via pioneer shrub to woodland is by no means simple or self-evident in dry sand dunes. Because of the high permeability of the substrate, salts (including calcium carbonate, sometimes abundantly present in young dunes) and other plant nutrients are easily washed out and lost in the subsoil. Most dune sands are derived from river sediments with a long geological history and have very little mineral reserve. Even where shrubs or woodlands have developed in relatively early stages of succession, there are many cases in which these are dying off at a certain stage and in the normal course of succession returning to herbaceous vegetation because of leaching of the soil, loss of humus or cumulative salt spray effects. On tops and slopes, water erosion also causes a loss of absorption capacity and nutrients of the soil profile. At the moment when the last traces of free lime are dissolved, soil pH quite suddenly turns from neutral to acid values. This is possibly detrimental to root nodules, essential for pioneer shrubs. Thus, there are some definite "turning points" in the processes within dune ecosystems which still require much research, but are clearly indicated by changes in the composition of vegetation.

11. Dense shrub in mature dunes

In favourable places pioneer shrub (zone 7) develops into higher and denser shrub with a more varied species composition. Moisture holding capacity and nutrient status of the soil, both closely connected with the thickness of the humus layer, are decisive in this respect. One of the most neglected but common causes of spatial differentiation in dry sand dunes is soil erosion caused by run off of rain water. In this way, top and slope profiles are decapitated, and succession in these parts is often retrogressive from more to less complicated structures. Gain of sand rich in humus at the foot of slopes, combined with an extra supply of rain water, is often correlated with progressive succession to high shrubs which for this reason occur in patches. As relief becomes levelled out in this way, the mosaic structure of the dune landscape becomes even more pronounced and complicated, and more difficult to explain in detail (DOING 1973).

12. Maritime forest on relatively rich soils

In cases similar to the shrubs of zone 11, forests may develop as a still later stage of succession or in even more favoured places. Shelter provided by high dunes, e.g. the "Wanderdünen" (PAUL 1944, 1953) described under zone 9, determines the potential height of these forests. In impoverished species composition and very limited height, they are sometimes found quite close to the beach, as far as soil conditions permit and especially where the cost is retreating. Except where the soil surface is unstable, dunes in climates where forests are the climax vegetation will not escape natural afforestation in the long run. This is a slow process in some cases, especially where the sand is chemically very poor. However, the floristic composition of these forests is usually different from that further inland, partly because of the salt spray effect. In warmer climates, even dominant trees may be specialised at this salt spray zone (OOSTING 1954).

13. Maritime forest on poor soils

Although dune succession in the xerosere is more prolonged and complicated on the finer and chemically richer soils than in the opposite case, impoverishment is unavoidable in the long run because of the fate of all psammic soils to be leached even in relatively dry climates. There is a striking difference in most areas between the maritime forest on relatively rich and that of poor soils, the former often being similar on sand dunes to that on substrates with a finer texture, and the latter mostly characteristic of sandy soils only, but not limited to the local climate of a narrow coastal strip.

14. Dune heaths

On well developed soil profiles in old "black" dunes (e.g. podsols), dune heaths are found in various areas. Like the forests of zone 13, these are often similar to comparable ecosystems of other sandy areas. By grazing or fire, heaths may be derived from forests, and in the absence of these disturbing influences return to forests. A development from communities of zones 8b or 9 directly to heath is also observed in some areas, and the immediate connection with a forest climax is sometimes doubtful in these cases.
Since heaths may be either present or absent on most latitudes, there is no clear connection with climate. Possibly their presence is related to a long history of fire as well as the chemically extremely poor, sandy soils in an area permitting evolution and migration of specific heath taxa.

3. Examples from specific areas

Although most landscape elements are found in most coastal areas where sand dunes are well developed, not all habitats are filled by specific plant communities in all areas. Sometimes these are filled by plants which have their optima in other communities, sometimes by introduced species and sometimes not at all.
As a general rule, species occurring in the more extreme environments of the zones at the beginning of the range, may also be found in the older or more sheltered situations after some form of disturbance. In this way, there is a

tendency to find increasing numbers of species going from the beach towards the inner border of a dune area, provided there are various zones with increasing length of succession history. In other words: the names of the species, mentioned for a certain zone, may be supplemented by most species of zones with lower numbers where disturbance takes place. The probability of occurrence of the latter species is roughly proportional to the proximity and ecological similarity of both zones. The order in which the zones have been placed, is therefore of the utmost importance for the proper interpretation of the scheme. Repetitions have been avoided as much as possible. In this way, the short floristic lists, in which only the most common or dominant species are mentioned do not represent plant communities or characteristic species, but "sociological species groups" = groups of species which have approximately the same range throughout the whole spectrum of plant communities. In some cases groups may occur almost alone, but more often they are found combined with one or more (sometimes many) other groups. They are mentioned under the number of the landscape element in which they play a prominent role for the first time in the order from 1-14 adopted in our scheme. In this particular element, they are to be regarded as "obligate" species, in all following numbers as "facultative" species. This arrangement is only valid for a certain part of a coast. Going along a coast, a change of climate often involves a switch of certain species groups from one zone to another, but the groups as such are largely unaltered, apart from possible limits of species areas.

A. *The eastern U.S. coast at* c. 35° N.L. (*North Carolina, Atlantic Ocean*)

Phytogeographically, this region extends from Cape Lookout in the south to Chesapeake Bay (Cape Henry) in the north. Literature: BURK 1962, COOPER 1975, GODFREY 1970, GODFREY and GODFREY 1976, OOSTING 1954, OOSTING and BILLINGS 1942, RADFORD et al. 1968.

1a. Annual tide mark ecosystems are developed on some beaches. Since rocky coasts with *algae* are missing in the area, tide marks are not very pronounced here, though. The main species are *Cakile edentula*, *Salsola kali* and *Euphorbia polygonifolia*.

1b. Some low, exposed parts of the foredunes may probably be interpreted as perennial tide mark ecosystems, with *Panicum amarum* and *P. amarulum* as domi-

nant grasses.

2a. Embryonic dunes, where present, are represented by a low foredune ridge c. 1-2 m high. Non-flowering *Uniola paniculata* is the major species here, towards the north (e.g. near Virginia Beach) replaced by *Ammophila breviligulata*. Both communities are monospecific in most places.

2b. Under the influence of enrichment by organic material, e.g. *Cenchrus tribuloides, Croton punctatus (Euphorbiaceae)* and *Heterotheca subaxillaris (Asteraceae)* occur.

3a. The foredune ridge is naturally relatively low in this area (c. 2 m, see GODFREY 1977) and frequently interrupted. This is probably partly connected with a lack of strength of average onshore winds and the frequent occurrence of hurricanes which cause breaks and areas of overwash. Where plantings are carried out, it is often higher (e.g. c. 5 m). The dominant, and often the only species is the optimally developed and abundantly flowering *Uniola paniculata*, a large grass, which is, however, not such a good sand binder as *Ammophila*. For this reason, *Ammophila* is often planted in the region immediately south of its natural occurrence.

3b. The main additional species, as usually favoured by enrichment of tide mark material, is *Solidago sempervirens*, a succulent composite with a large range (e.g. extending much further north) which also occurs on tide marks in high salt marshes and on rocky coasts (e.g. in Maine).

4. In sheltered situations within the foredune zone, *Strophostyles helvola (Fabaceae), Oenothera humifusa* and *Hydrocotyle bonariensis (Apiaceae)* are common species among the *Uniola*. This zone is mostly narrow, e.g. < 50 m.

5. As mentioned under 3, areas of overwash are very important in this region, especially in its southern part. In some places they replace the foredunes, which have been levelled by storm surges here. The major species is *Spartina patens* (which is also found in high salt marshes), locally accompanied by e.g. *Fimbristylis spadacea.*

6. General salt spray vegetation is represented by a low open shrub, mostly in dune slacks, with *Iva imbricata, I. frutescens* and *Baccharis halimifolia*, all *Asteraceae* and the latter 2 also found in the highest salt marshes. Rocky coasts are absent in the area.

7. Pioneer dune shrub is mainly formed by two evergreen species: *Myrica cerifera* and *Ilex vomitoria*, the former with root nodules supplying nitrogen.

8. No calcareous dune areas have been observed by the author from Cape Hatteras northwards, and communities of zone 8 seem to be missing there. They are more or less replaced by weedy vegetation with e.g. *Gaillardia* sp.

9. Small blowouts are common in most dune complexes, and in connection with the acidity of the sand distinct ("steppe-like") communities are developed here, consisting in this case mainly of the bunch grass *Andropogon scoparius*. The typical blowout habitat, as described in the second part of this paper, is according to the author's opinion, more important for the occurrence of these communities and the absence of *Uniola*-communities than the amount of salt spray (OOSTING and BILLINGS 1942).

10. Especially in places where dune erosion takes place, small steep bluffs or hummocks are found with dense vegetation of mostly lianas.

10a. In young dunes, often close to the beach, *Rhus radicans* and *Parthenocissus quinquefolia* are often found in this habitat without accompanying shrub species.

10b. In somewhat older dunes, woody vegetation with *Rhus copallina* (a shrub or miniature tree), *Vitis* sp. and *Smilax* sp. *(Liliaceae)* occur in similar clumps.

11. The major species of the more advanced stages of shrub and woodland development is *Juniperus virginiana*. In some places, *Juniperus silicicola* or *Persea borbonia (Lauraceae)* are found here.

12. Where conditions are sufficiently stable, e.g. in the shelter of wide dunes at Buxton Woods (Cape Hatteras, N.C.) or high dunes at Nags Head (further north), a type of maritime forest is found on the richer soils which originally was much more widespread, but was destroyed in many areas by man.

Major species are *Quercus virginiana* (relatively salt-resistant) or *Q. laurifolia*, and *Ilex opaca* (all evergreen), accompanied by e.g. *Tillandsia usneoides (Bromeliaceae)*, *Sabal minor* (the palm which extends most northwards), *Osmanthus americana (Oleaceae)*, *Zanthoxylon clava-herculis (Rutaceae)*, *Morus rubra*, *Acer rubrum* and in the undergrowth e.g. *Mitchella repens (Rubiaceae)*. Further south, *Sabal palmetto* and *Serenoa repens*, two salt resistant palms, become prominent in the rich maritime forest.

13. On poor soils in sheltered places, possibly corresponding with soil development which has started under the conditions described at zone 9, pine forests are found with *Pinus taeda*, *Quercus laevis*, *Lonicera japonica*, *Aralia spinosa*

and *Vaccinium arboreum*. As those of zone 12, these forests are mostly rich in lianas (those mentioned for zone 10). Moreover, mixtures of the species mentioned for zones 12 and 13 are common in some areas.

14. Dune heath communities are absent in the region.

B. *The eastern U.S. coast at c. 42° N.L. (Massachusetts, Atlantic Ocean)*

Similar conditions are found from Chesapeake Bay (Cape Charles) to southern Maine (Portland). Literature: CARLOZZI et al. 1975, GODFREY 1970, GRANDTNER 1978, LAMOUREUX and GRANDTNER 1977, 1978.

1a. The annual tide mark communities are not much different from those of region A: *Cakile edentula, Salsola kali* and *Euphorbia polygonifolia* are the most common species.

1b. The main species of perennial tide mark communities is *Honkenya peploides*. Still further north, *Elymus mollis* occurs in this zone (TüXEN 1966).

2a. Embryonic dunes are mainly colonised by low and non-flowering *Ammophila breviligulata*, in contrast to most other areas, where the species of zones 2a and 3a are different.

2b. The most frequent additional species on "enriched" sites are *Solidago sempervirens, Artemisia stelleriana,* and (locally) *A. caudata*. The second species extends southwards into region A and is also planted in some areas.

3a. Foredunes are in most cases much higher in this region than in the former one, partly because of the effectiveness of *Ammophila breviligulata* (which has its optimum in this zone), and in some areas also because of greater availability of sand or the strength and direction of prevailing winds.

3b. Additional species in chemically favoured places are the same as those already mentioned for zone 2b.

4. In sheltered foredunes, *Lathyrus japonicus* is common as probably the most widely distributed dune plant in cool temperate areas of the world. A second important species is *Festuca rubra* (cf. C4).

5. Areas of overwash are much less prominent here than in the former region. Where they occur, *Spartina patens* sometimes plays a similar role as there, but it extends far more northwards as a salt marsh than as a dune species. In other places *Agropyron repens* (introduced from Europe) is found in this habitat type.

6. As representatives of this zone, the deciduous *Prunus maritima* and *Rosa*

rugosa (introduced from N-Japan) are found, both highly resistant to soil surface instability and in this way also occurring as pioneer shrubs, possibly replacing *Myrica* (zone 7) on somewhat richer soils.

7. Dominant as a pioneer shrub in the whole area is the deciduous *Myrica pensylvanica*, with root nodules aiding in nitrogen supply of the ecosystem. This is a species of acid soils.

8. As in the former region, this zone seems to be missing in the area because of the acidity of the sand.

9. Communities of blowouts and other dry, sterile sands are well developed and consist of *Hudsonia tomentosa* (often dominant), *H. ericoides* (both heath-like chamaephytes from the family *Cistaceae*), *Andropogon scoparius*, *Carex artitecta*, *Deschampsia flexuosa*, *Cladonia* div. sp. and some dwarf plants like *Cyperus grayii* and *Hypericum gentianoides*. There is a striking similarity of this habitat to that of the European *Corynephoretum canescentis*, combined with a wide difference in physiognomy and floristic composition of the vegetation.

10a. Bluffs and hummocks of eroding dunes are similar to those in the former region, with *Rhus radicans* and *Parthenocissus quinquefolia*.

10b. Similar situations in older stages of succession are indicated by *Rhus copallina*, *Smilax rotundifolia* and *Prunus serotina*. The latter is found here as a shrub with remarkable resistance to extreme environmental conditions.

11. Dense shrub is well developed in many sheltered places and consists mainly of *Juniperus virginiana*, *Rosa carolina*, *Amelanchier canadensis*, *Berberis vulgaris* (on the richer soils, introduced from Europe) plus *Vitis rotundifolia* and other lianas.

12. A deciduous hardwood forest with e.g. *Quercus velutina*, *Q. rubra*, *Sassafras albidum*, *Acer rubrum*, *Nyssa sylvatica*, *Fagus grandifolia* or *Populus tremuloides*, is found where disturbance has been minimal for a sufficiently long period. Unlike the "salt spray climax" of the warm-temperate region, its composition is not much different from that of forests on equivalent soils further inland. Further north (e.g. in northern Maine) these forests are replaced by dense coniferous forests with e.g. *Picea rubens* and *Abies balsamea*.

13. On poor soils, such as reworked pleistocene sands or in environments derived from the habitats of zone 9, open coniferous or low deciduous forests have

developed with e.g. *Pinus rigida, Quercus ilicifolia, Betula papyrifera* and an undergrowth with various *Ericaceae*, e.g. *Kalmia angustifolia, Vaccinium corymbosum* or *Gaylussacia* sp.

14. Heath-like types of vegetation are found in this region, which are poor in species, viz. mainly *Arctostaphylos uva-ursi* and *Corema conradii (Empetraceae)*. Further north (GRANDTNER 1977) *Empetrum nigrum* becomes prominent.

C. *Western France at c. 46° N.L. (Département Vendée, Bay of Biscay)*

At comparable latitudes, summers are similar but winters are much milder on western European coasts than in the eastern U.S. The boundary between the cool and warm temperate belts, indicating a similar length of the growing season, is found at the U.S. coast at ca. 37° N.L., in France at ca. 48° N.L. The difference in latitude between the southern boundaries of dense coniferous forests is even greater. The amount of annual rainfall, and even more so that of summer rains, is much higher on the U.S. coast. Western European coasts are (except those of the eastern coasts of the British Isles) more exposed to prevailing winds from the sea. Most western British dunes, and those of the continent between the Gironde and Bergen (province of North Holland) are calcareous. This factor is partly responsible for relatively rich floras and great variation in vegetation. Western European dunes have been studied by numerous authors (Literature: BAKKER 1976, GEHU 1969, GEHU and TÜXEN 1975). The scheme given below is mainly intended as a framework for comparisons with other parts of the world.

1a. The development of tide mark communities is favoured in western France by the presence of rocky coasts with zonations of *algae* etc. and of many curved and stable beaches of limited length, sometimes combined with river entrances. The main species of annual tide marks on sandy beaches are *Cakile maritima, Salsola kali* and *Atriplex arenarius.*

1b. Perennial tide marks are mainly colonised by *Honkenya peploides*. From Normandy northwards, *Elymus arenarius* plays an increasing role here.

2a. Embryonic dunes are present on stable or growing coasts in the form of a low and more or less continuous foredune ridge ca. 2 m high, where *Agropyron junceiforme* is the characteristic, optimally developed and often the only species.

2b. A long growing season and the availability of organic matter favour the growth of the additional species *Eryngium maritimum, Calystegia soldanella* and *Euphorbia paralias*, which grow abundantly here and in the foredunes (zone 3) of this region.

3a. The yellow dunes, mostly a ridge of 5 m high or more, owe their existence and resistance mainly to *Ammophila arenaria*, the most successful of all known dune building grasses.

3b. For the same reasons as mentioned under 2a, a number of additional species are commonly found in favoured localities, mainly *Matthiola sinuata (Brassicaceae), Medicago marina* and *M. litoralis (Fabaceae), Diotis candidissima (Asteraceae)* and *Euphorbia polygonifolia* (introduced from America).

4. Communities on the inner slope of the foredunes and on the low dunes often present in a strip behind these are also well developed in this area. Apart from non-flowering *Ammophila* (which may still occur as a local dominant here) there is e.g. *Festuca rubra* var. *arenaria, F. juncifolia, Artemisia lloydii* and *Galium arenarium.*

5. Since barrier beaches and transitions to salt marshes are not common in the region, overwash areas are rare. Species occurring in this type of habitat are *Agropyron pungens, A. repens, Agrostis stolonifera, Juncus acutus, Carex serotina, Beta maritima* and *Glaux maritima.*

6. The relatively warm and dry summers in the region are favourable for the development of specific salt spray communities, with *Crithmum maritimum (Apiaceae), Silene thorei, Daucus maritimus* and *Herniaria maritima (Caryophyllaceae).*

7. Climate (see under 6) is not favourable for pioneer shrubs. These are largely replaced by communities of zone 8. A more or less woody, but low chamaephytic species common in the zone where further northwards *Hippophaë* could be expected is *Helichrysum stoechas (Asteraceae).*

8a. In young, calcareous dunes, where *Ammophila* is diminished because of reduced influx of sand, low, open communities, rich in mosses and annuals, are developed, forming characteristic and attractive communities. Some of the most important species are: *Phleum arenarium (Poaceae), Dianthus gallicus (Caryophyllaceae), Alyssum calycinum (Brassicaceae), Euphorbia portlandica* and the mosses *Tortula ruraliformis, Pleurochaete squarrosa* and *Ceratodon conicus.*

8b. Following 8a as a successional stage, communities are found that are even richer in species, covering the superficially humus rich sand nearly completely. Major species are e.g. *Koeleria arenaria, Allium sphaerocephalum, Rosa pimpinellifolia* and the moss *Hypnum cupressiforme* var. *lacunosum*.

9. On sterile, acid sands, widespread e.g. south of the "lime boundary" (the Gironde embouchure) communities are dominated by *Corynephorus canescens (Poaceae), Carex arenaria, Jasione montana, Helianthemum guttatum, Armeria plantaginea (Plumbaginaceae)*, the moss *Polytrichum juniperinum* and various lichens, mainly *Cladonia* sp.

10a. The relatively dry summers are not favourable for the widespread occurrence of communities indicating increased mineralization of humus. Such places are indicated mainly in zone 8a by *Lagurus ovatus (Poaceae)* and in zone 8b by *Ephedra distachya (Gnetaceae)*.

10b. The type of environment mentioned above is favourable for the development of deciduous shrubs on stable north slopes with *Ligustrum vulgare, Rubus ulmifolius, Polypodium vulgare* and *Clematis vitalba*.

11. The realisation of favourable conditions for the development of dense shrubs is even more difficult than in the case of pioneer shrubs. The only species occurring as such is the evergreen *Quercus ilex*, shorn by the sea wind.

12. The main species of the rich maritime forest, mostly restricted to the innermost slopes of the dunes, are *Quercus robur, Q. pubescens* (both deciduous), *Ruscus aculeatus (Liliaceae), Rubia peregrina, Hedera helix (Araliaceae), Iris foetidissima* and *Cephalanthera rubra (Orchidaceae)*.

13. Pine forests are planted on a large scale, especially in the acid dunes of "les Landes". For this reason, their natural occurrence is difficult to judge. Important species are e.g. *Pinus pinaster, Lonicera periclymenum, Pteridium aquilinum* and *Deschampsia flexuosa (Poaceae)*.

14. Dune heaths are only found in areas of primarily acid dunes, the calcareous dune areas not being extensive and old enough to attain a stage of intensive leaching. Major species are e.g. *Erica cinerea, Calluna vulgaris* and *Ulex gallii*.

D. Southeastern Japan at c. 33° N.L. (Kyushu, Pacific Ocean)

Climatically, the eastern coast of Japan is much more similar to that of the U.S. than to the western European coast. Summers are warm and humid, at least in the south, and winters are relatively cold and rich in snow. However, the belt of deciduous forests is narrow in Japan, since evergreen "laurel-leaved" forests are extending far northwards, especially along the eastern coast of Honshu, and dense needle-leaved coniferous forests are found at relatively low latitudes and altitudes on Hokkaido. (Literature: NAKANISHII and SUZUKI 1973, OHBA et al. 1973, OHWI 1965).

1a. Since most sand dune areas are relatively small and stable, bordering on rocky coasts, tide mark ecosystems are well developed in many localities. The major annual species in most places is *Salsola komarovii*, locally *Atriplex gmelinii*.

1b. In addition to the factors mentioned under 1a, beach vegetation is favoured by relatively low average wind velocities and a humid climate. Perennial tide mark zones are therefore unusually well developed for an extratropical region, mainly consisting of the species *Calystegia soldanella, Lathyrus japonicus, Glehnia littoralis (Apiaceae), Ixeris repens (Asteraceae)* and *Linaria japonica*. It is also remarkable that the first two species occur abundantly in a more exposed location here than in other parts of their area in the northern hemisphere.

2a. Embryonic dunes are well developed where the coast is sufficiently stable, forming a low foredune ridge of 1-2 m high. They are colonised by (often non-flowering) *Carex kobomugi*.

2b. Additional species in this zone are the same as those mentioned under 1b.

3a. The main foredune ridge is mostly low (e.g. c. 5 m) and occupied by *Carex kobomugi* in its optimal (flowering) form. This species is not capable of building high dunes by the fixing of a large percentage of overblowing sand.

3b. Additional species are the same as those of zone 1b and 2b.

4. On the sheltered slopes of foredunes and in the zone immediately behind there is a distinct plant community, consisting mainly of *Ischaemum anthephoroides* (a high perennial grass), *Wedelia prostrata (Asteraceae)* and *Carex breviculmis*.

5. Overwash situations are not common, but well developed in some places and distinguished by *Zoysia macrostachya (Poaceae)* and *Carex pumila*.

6. Evergreen salt spray shrubs, similar to those on rocky cliffs, are mainly formed by *Pittosporum tobira*, accompanied by e.g. *Rhaphiolepis umbellata (Rosaceae)* and *Euonymus japonicus*.

7. Pioneer shrubs are represented in this area by *Vitex rotundifolia (Verbenaceae)* or *Juniperus conferta*.

8. Communities of open grassland, comparable to those of e.g. western France, are scarcely developed. This is the more remarkable, since much of the dune sand is of volcanic origin, and therefore chemically relatively rich. Perhaps its dark colour is an unfavourable factor for the colonisation of bare patches by small plants.

9. Communities of blowouts and comparable sterile sands are not common, but can sometimes be distinguished by a special series of species. These are *Fimbristylis sericea* and *Bulbostylis barbata* (both *Cyperaceae*) and the mosses *Rhacomitrium canescens* and *Polytrichum* sp., also by *Cladonia* sp.

10a. Special communities linked to young dunes with increased decomposition of organic matter are not clearly distinguishable. Perhaps *Messerschmidia sibirica (Boraginaceae)* is an indicator of such conditions.

10b. In older dunes on acid sand, places where shrubs or trees have died off are invaded by a community with *Imperata cylindrica, Pteridium aquilinum* and *Miscanthus sinensis (Poaceae)*.

11. Dense shrubs are restricted to sheltered places behind a relatively wide dune strip. Major species are *Elaeagnus umbellata* and *Rosa wichuraiana*, with *Viola mandshurica* as a small herb.

12. On relatively rich soils, evergreen forest fragments may be found with e.g. *Neolitsea thunbergii (Lauraceae), Celtis sinensis, Elaeagnus macrophylla, Camellia japonica* with an undergrowth of e.g. *Paederia scandens (Rubiaceae)* and *Cyrtomium falcatum (Polypodiaceae)*.

13. The true maritime forest consists mainly of *Pinus thunbergii*, with e.g. *Zanthoxylon piperitum (Rutaceae)* and *Lonicera japonica*.

14. Dune heaths are missing in southern Japan. The widespread dominance of soils derived from volcanic rocks and ashes is prohibitive for the development of podsolic soils and heath communities in general in this region.

E. *Southeastern Australia at* c. 35° S.L. (*New South Wales, Pacific Ocean*)

The climate of this coast differs from all others discussed here by its practically frost-free winters, indicated e.g. by the occurrence of mangroves (mainly *Avicennia marina*). The climate can be indicated as warm-temperate, and climax vegetation on rich soils is a temperate rainforest with some subtropical species. Literature: BIRD 1965, BEADLE et al. 1972, COALDRAKE 1961, PIDGEON 1940.

The coast of eastern Australia consists of a great number of smaller or larger bays, many with permanent or temporary river entrances and rocky headlands of variable geological origin. All types of coastal vegetation (sand dunes, cliffs, salt marshes and mangroves) can be studied here in many well developed examples in various climatic zones and phytogeographic regions (DOING 1970).

1a. As a result of the natural conditions of the coast, tide marks are mostly well developed on eastern Australian beaches. However, in the temperate region there are scarcely any native species, and no vegetation types, to fill this niche. Annual communities consist of *Cakile edentula* (introduced from America), further south of *C. maritima* (from Europe) and *Salsola kali* (probably from Europe).

1b. Perennial tide mark communities are also found in many places and mainly consist of introduced species: *Arctotheca populifolia* (*Asteraceae*, introduced from South Africa), with small quantities of native species, mainly *Atriplex cinerea* (a woody species!) and *Euphorbia sparrmanii* (a decumbent annual species).

2a. Embryonic dunes are relatively stable because of moderate wind velocities and a long growing season. There is mostly a low, continuous foredune ridge (e.g. 1-2 m high). The top of this ridge is the zone where the grass *Spinifex hirsutus* is optimally developed. In the front of this, there is sometimes a gently sloping zone with non-flowering *Spinifex*. This species has only moderate sand binding capacities, more comparable with those of the southern Japanese *Carex kobomugi* or the western North-American *C. macrocephala* than with those of *Ammophila arenaria*, which is often planted in the southern part of the area. Also in the south, the native *Festuca littoralis* is characteristic of this zone, especially on calcareous sand.

2b. Common additional species with a preference for enriched habitats are mainly *Sonchus megalocarpos*, *Senecio spathulatus* and *Calystegia soldanella* (which is native here and therefore has a distribution along temperate coasts of both hemispheres).

3a. Normally, there is a second foredune ridge, ca. 3-6 m high, where most of the sand is deposited which is not fixed in the *Spinifex*-zone. The main species here is *Acacia sophorae*, an evergreen, creeping "wattle" with phyllodes and nitrogen fixing root nodules, c. ½-1 m high.

3b. The *Acacia sophorae* shrub is mostly poor in species. As common additional plants *Stephania japonica (Menispermaceae)*, *Clematis glycinoides (Ranunculaceae)* and *Hibbertia scandens (Dilleniaceae)* might be mentioned.

4. Immediately behind the *Acacia*-zone there is usually a higher shrub (ca. 2-3 m) of *Leptospermum laevigatum (Myrtaceae)*, often mixed with smaller numbers of *Phyllanthus gasstroemii (Euphorbiaceae)*, poor in other species and in undergrowth (e.g. *Viola hederacea)*. It should be noted that two different evergreen shrub zones are developed on these coasts occurring in habitats which are occupied mainly by herbaceous vegetation in all other temperate regions discussed here.

5. Dry overwash areas are found on high, sheltered beaches and at the back of sand dunes in estuaries etc. The main characteristic species of this habitat are *Carex pumila*, *Aster subulatus* and *Juncus acutus* (the latter introduced from southern Europe).

6. Salt spray shrubs are well developed in the area, mainly on rocky coasts, and they have many characteristic species, e.g. *Westringia fruticosa (Lamiaceae)*.In the dunes, they are mainly found on calcareous sand, mostly replacing *Acacia sophorae* shrub, and consist of *Correa alba (Rutaceae)*, *Leucopogon parviflorus (Epacridaceae)*, both mainly restricted to sand dunes, and *Rhagodia baccata (Chenopodiaceae)* and *Myoporum insulare (Myoporaceae)*, both "general" salt spray species.

7. As a third zone of evergreen woody vegetation, a woodland (c. 6-10 m high) is well developed even in comparatively narrow dune areas. The main species is *Banksia integrifolia (Proteaceae)*, accompanied by *Casuarina glauca* (a salt tolerant tree also found on cliffs and at the upper margin of salt marshes), *Monotoca elliptica* (a shrub of the family *Epacridaceae*) and *Geitonoplesium cymosum* (a winding, herbaceous evergreen of the familiy *Philesiaceae*).

8. Open grassland communities, rich in annuals, are not well developed in undisturbed dry dunes, possibly in connection with the fact that calcareous sands are rare in the area, like on sheltered (mostly eastern) temperate coasts in general.

8a. On patches of bare, but more or less stable sand, species like *Crassula sieberana, Polycarpon tetraphyllum (Polygonaceae), Tortella calycina* and *Ceratodon purpureus* can be placed into the category corresponding with e.g. communities of *Tortula ruraliformis* in western Europe. Some species, introduced from Europe, may also be present, e.g. *Medicago minima.*

8b. Grassland communities, representing a later stage of succession than 8a, are also uncommon, and not much different in composition from native grasslands on other sandy soils in the same area. Species include *Themeda australis* (a very common grass in many areas, comparable in its range of habitats to *Miscanthus sinensis* in Japan), *Danthonia setacea (Poaceae) Poa* sp. or *Kennedia prostrata (Fabaceae).*

9. As in other dune areas, blowouts occur in all zones and of all sizes. This zone is filled in southwestern Australia nearly exclusively by *Spinifex hirsutus*, the same species that colonises the first, frontal dune ridge there. The way in which "wounds" in the dune landscape are "healed" by a perennial graminoid extending its rootstocks, from which leaf-tufts are rising up in regular rows, is comparable to the behaviour of *Carex arenaria* on European dunes.

10. In contrast to habitat type 9, distinct communities on eroding dunes and patches of dying shrub etc. are well developed in the area.

10a. In young, unstable dunes, the "succulent mat", consisting of *Carpobrotus aequilateris (Aizoaceae), Lomandra longifolia (Xanthorrhoeaceae), Scaevola calendulacea (Goodeniaceae), Pelargonium australe (Geraniaceae), Cassytha melantha* and *C. glabella* (twining, leafless *Lauraceae*) is a well known phenomenon occurring in various zones, but mostly on restricted surfaces.

10b. In more stable dunes, where erosion is serious, e.g. caused by recreation, a shrubby community indicates intensified mineralisation of organic matter. Main species are *Chrysanthemoides monilifera (Asteraceae,* introduced from South Africa) and *Lantana camara* (introduced from tropical South America). In similar places in older dunes with acid sand, *Imperata cylindrica* (native) and *Pteridium esculentum* are found.

11. Only in old dunes with chemically impoverished sand there are shrub communities which differ from those of zones 3, 4 or 6. They are found in a limited number of localities and consist e.g. of *Acacia longifolia* (similar to *A. sophorae* but with an upright growing habit and c. 2-4 m high), *Banksia serrata, B. ericifolia (Proteaceae), Cassinia aculeata (Asteraceae).*

12. Because of the heavy surf of the southern Pacific Ocean and the frequency of sea winds, the effect of salt spray extends relatively far inland in southeastern Australia. Climax vegetation on comparatively rich dune sands and on other substrates (e.g. various types of weathered rock) in a strip of coast approx. 1-2 km wide in exposed areas is a forest of *Eucalyptus botryoides*, with *Acmena smithii (Myrtaceae), Elaeodendron australe (Celastraceae), Billardiera scandens (Pittosporaceae)* etc.

13. The composition of climax forests on dry, poor, acid soils is quite different and not characteristic of the salt spray zone. The tree layer is often dominated by *Eucalyptus maculata*, an important undergrowth species is sometimes *Macrozamia communis (Zamiaceae)*. Further south, the main tree species is *Eucalyptus viminalis*, further north it is *E. pilularis*.

14. On podsolic soils in old dunes, the effect of fire causes "degradation" of forests of zone 13, first into shrub communities (zone 11), after repeated burning into heath communities. These are well developed and rich in species in some areas, consisting of e.g. *Correa reflexa (Rutaceae), Ricinocarpus pinifolius (Euphorbiaceae), Haloragis teucrioides, Hibbertia* div. sp. *(Dilleniaceae), Leucopogon ericoides (Epacridaceae), Bossiaea ensata (Fabaceae), Dillwygnia glaberrima (Fabaceae), Actinotus helianthi (Asteraceae).*

4. Summary and conclusions

Of the various ways, open for the comparison of vicarious plant communities in different floristic kingdoms or regions of the earth, a division of major landscapes into "landscape zones" or "habitat types" has been adopted in this paper for dry coastal sand dunes. From studies in various continents, a division into 14 of such zones was derived. These are described for the eastern U.S., western European, southern Japanese and southeastern Australian coasts.

The habitat types are:

1. Tide mark zone on sandy beaches.
   a. Annual communities.
   b. Perennial communities.

2. Embryonic dunes (beach dunes).
   a. Monospecific communities.
   b. "Enriched" communities.
3. Yellow dunes with sand accretion (foredunes).
   a. Monospecific communities.
   b. "Enriched" communities.
4. Sheltered zone immediately behind foredunes.
5. Sandy flats created by "overwash".
6. Specific salt spray vegetation (e.g. on dune cliffs).
7. Open pioneer dune shrub or woodland zone.
8. Dry, short, open dune grassland on calcareous sand.
   a. Herbaceous communities rich in annuals.
   b. Communities rich in mosses (sometimes with chamaephytes).
9. Gray dunes (e.g. blowout communities) on sterile sand.
10. Ecosystems with increased mineralisation of organic matter in the topsoil.
   a. Young, calcareous dunes with herbaceous vegetation (e.g. on bluffs or hummocks).
   b. Older dunes with woody vegetation.
11. Dense shrub in mature dunes.
12. Maritime forest on relatively fertile soils.
13. Maritime forest on poor, acid soils.
14. Dune heath ("black dunes").

In general, species which have their major distribution in a certain zone, may occur locally in zones with higher numbers as a result of various types of disturbance.
In this way, it is possible to compare local topographical, climatological and phytogeographical conditions in various regions and draw some general conclusions about their relationships to the structural and floristical composition of the communities. Some problems, that can be formulated on the basis of this approach are concerned with the shift of single plant species or species groups in relation to comparable zones in different climatic regions, the degree of saturation of ecological niches by native species and the distribution of introduced species which sometimes fill available niches. General trends may be discerned in species numbers, taxonomic and life form spectra within the same habitat type in different regions. Various interrelationships are pointed out, e.g. between the geomorphology of dune areas, climatic conditions (wind force and direction, aridity), composition of the sand (content of calcium carbonate and organic matter), plant communities and the properties (e.g. size, woodyness) of dominant species. Critical ecological factors for the delimitation of communities and successional relationships between landscape zones may also be traced in this way. These are often more difficult to evaluate only by means of analytical studies of populations or measurements of single environmental factors. Finally, existing classifications of plant communities can be supplemented in this way by a classification of ecosystems or "geosystems", providing a framework for a better formulation of fundamental as well as applied ecological problems (e.g. management and conservation of sand dune areas).
Landscape studies (including vegetation maps) in other types of extreme environments (e.g. mangroves and salt marshes, aquatic communities, alpine communities), as well as in catenas with climax or secondary vegetation may lead to similar comparisons in carefully selected areas.

Zusammenfassung und Schlussfolgerungen

Aus den verschiedenen Möglichkeiten, Vergleiche anzustellen zwischen vikarierenden Gesellschaften in verschiedenen Florareichen oder -regionen der Erde, wurde für die trockenen Küstendünen eine Einteilung gewählt in "Landschaftszonen" oder Biotope. Aus Studien in mehreren Erdteilen wurden 14 solcher Zonen abgeleitet und beschrieben für die östlichen V.S., West-Europa (Frankreich), Süd-Japan (Kyushu) und Südost-Australien (New South Wales).

Dieses Schema enthält:

1. Flutsäume auf Sandstrand.
   a. Einjährige Gesellschaften.
   b. Mehrjährige Gesellschaften.
2. Embryonaldünen (Stranddünen).
   a. Artenarme Gesellschaften.
   b. "Angereicherte" Gesellschaften mit mehreren Arten.
3. Weissdünen mit Sandanflug.
   a. Artenarme Gesellschaften.
   b. "Angereicherte" Gesellschaften mit mehreren Arten.
4. Anflugzone im Schutz der Weissdünen.
5. Durch Ueberspülung mit Sand bei Hochflut zustandegekommene trockene Ebenen.
6. Spezifische Gesellschaften der Salz-Sprühzone (z.B. auf Dünenkliffen).
7. Offene Pioniergebüsche oder Wäldchen.
8. Kleingrasdünen auf kalkhaltigem Sand.
   a. Offene Gras- und Kräutergesellschaften mit einjährigen Arten.
   b. Moosreiche Gesellschaften (manchmal mit Chamaephyten).
9. Graudünen (z.B. in Windkuhlen) auf sterilem Sand.
10. Oekosysteme mit verstärkter Mineralisation von organischer Substanz im Oberboden.
    a. In jungen, kalkreichen Dünen mit krautartiger Vegetation (z.B. Kupsten).
    b. In älteren Dünen mit Gebüschen oder Wäldern.
11. Dichte Gebüsche in fixierten Dünen.
12. Küstenwälder auf reicheren Böden.
13. Küstenwälder auf ärmeren Böden.
14. Dünenheiden ("Schwarzdünen").

Im Allgemeinen können Arten, welche in einer bestimmten Zone optimal entwikkelt sind, infolge Störungen verschiedener Art in höher numerierten Zonen auftreten.
Auf diese Weise war es möglich, die lokalen topographischen, klimatologischen und pflanzengeographischen Verhältnisse in verschiedenen Regionen auf sinnvolle Weise miteinander zu vergleichen und einige allgemeine Schlussfolgerungen über ihre Beziehung zur Struktur und floristischen Zusammensetzung der Pflanzengesellschaften zu ziehen. Einige Probleme, die sich daraus ergeben, sind z.B. der Zonenwechsel von bestimmten Arten oder Artengruppen mit grösseren Arealen im Zusammenhang mit Klimawechsel, der Sättigungsgrad ökologischer Nischen mit einheimischen Arten und die Verbreitung von Adventivarten, welche manchmal offene Nischen füllen können. Innerhalb derselben Zone in den verschiedenen Regionen lassen sich allgemeine Tendenzen in Artenzahlen, taxonomischen und Lebensformen-Spektren erkennen. So können z.B. Wechselbeziehungen zwischen der Geomorphologie von Dünengebieten, des Grossklimas

(Windstärke und -richtung, Aridität), der Zusammensetzung des Sandes (Gehalt an Kalk und organischer Substanz), den Pflanzengesellschaften und den Eigenschaften (z.B. Grösse, Holzigkeit) der dominierenden Arten erkannt werden. Auf diese Weise können auch die kritischen ökologischen Faktoren für die Abgrenzung der Gesellschaften und die dynamischen Beziehungen zwischen den Landschaftszonen aufgefunden werden. Nur aufgrund von analytischen Populationsstudien oder Messungen einzelner Umweltfaktoren sind diese oft schwieriger zu beurteilen. Schliesslich kann man auf diese Weise die existierenden Klassifikationen von Vegetationseinheiten mit einer Einteilung von Oekosystem- oder "Geosystem"-Typen ergänzen. Dies könnte als Beitrag zu einer besseren Formulierung von theoretischen und praktischen ökologischen Problemen (z.B. in Bezug auf Verwaltung und Schutz von Dünengebieten) dienen.
Landschaftsstudien (einschliesslich Vegetationskartierungen) können sowohl bei extremen Umweltbedingungen (z.B. Mangroven und Salzwiesen, Wasserpflanzengesellschaften, alpine Gebiete) als auch in "Catenas" mit natürlicher oder sekundärer Vegetation auf gleichartige Weise zu Vergleichen zwischen sorgfältig ausgewählten und umgrenzten Gebieten führen.

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